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Influence of Natural and Anthropogenic Environmental Variability on Larval Fish Diet, Growth, and Condition in the Northcentral Gulf of Mexico

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INFLUENCE OF NATURAL AND ANTHROPOGENIC ENVIRONMENTAL VARIABILITY ON LARVAL FISH DIET, GROWTH, AND CONDITION IN THE NORTHCENTRAL GULF OF MEXICO

by

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ABSTRACT

The northern Gulf of Mexico experiences high levels of freshwater runoff annually from various sources including the Mississippi River and Mobile Bay, among other sources. Early life history stages of fishes are especially vulnerable to environmental variability created by freshwater discharge. The objectives of this study were to describe the available prey field, diet, growth and condition of larval fishes with respect to various effects of freshwater discharge in the northern Gulf. The first chapter compared these parameters in larval Gulf Menhaden (*Brevoortia patronus*) collected from three different water masses characterized by physical and biological parameters after the opening of the Bonnet Carré Spillway in January 2016. Zooplankton community structure was found to be significantly different among the water masses. Larval Gulf Menhaden diet did not differ significantly among the water masses, but larvae from the Chandeleur Sound region had significantly lower recent growth and poorer condition than larvae from the other regions. The second chapter addressed the same parameters in Atlantic Bumper (*Chloroscombrus chrysurus*) in relation to summer-time hypoxia. Although found in a reduced habitat, the larvae collected above hypoxia did not experience differences in prey field, diet, growth, or condition based on morphometric analyses. Overall, my studies exemplify how difficult it is to predict results of environmental variability on larval fishes.

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DEDICATION

I would like to dedicate this thesis to my parents, for instilling the importance of knowledge in me, and for always believing in my abilities.

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LIST OF ABBREVIATIONS

GoM	Gulf of Mexico
BCS	Bonnet Carré Spillway
SL	Standard Length
SIMPROF	Similarity Profile
ANOSIM	Analysis of Similarity
SIMPER	Similarity Percentage
MDS	Multi-dimensional Scaling Analysis
BIONESS	Bedford Institute of Oceanography Net Environmental Sampling System
PCA	Principal Component Analysis
PC	Principal Component
NL	Notochord Length
DA	Depth at Anus
DPF	Depth at Pectoral Fin
HL	Head Length
HH	Head Height
ED	Eye Diameter
LJL	Lower Jaw Length

CHAPTER I - INTRODUCTION

The northcentral Gulf of Mexico (GoM) is a river-dominated coastal region that receives freshwater from multiple sources. The dominant riverine discharge comes from the Mississippi River, and the majority of this freshwater input flows out of the Birdsfoot delta and then west toward Texas and offshore (Dinnel and Wiseman 1986). East of the Birdsfoot delta, much of the freshwater discharge is sourced from Mobile Bay, local lakes (e.g., Lake Pontchartrain), and smaller river systems (e.g., Biloxi River) (Sikora and Kjerfve 1985). Collectively, the region stretching from Sabine Pass at the Texas-Louisiana border to Mobile Bay is known as the Fertile Fisheries Crescent (Gunter 1963); the nutrient-laden freshwater inputs stimulate high biological productivity, and as a result, the region is responsible for approximately 70-80% of all fisheries landings in the northern GoM (NMFS 1998, Grimes 2001).

Freshwater input can have a variety of impacts on coastal systems. Nutrients such as nitrogen and phosphorous are normally limited in marine environments (Bianchi et al. 2010). Increased levels of nutrients delivered by freshwater discharge, therefore, stimulate primary production, which can alter local trophic systems based on the amount and type of phytoplankton that become dominant in the area (Officer and Ryther 1980, Turner et al. 1998). Furthermore, freshwater can alter the physical parameters of the water column. Freshwater discharge enters the marine environment as a cooler, less saline, buoyant layer (Rabalais et al. 2002). As a result, community structure may shift based on the temperature and salinity tolerances of the species present (Barletta et al. 2005). This freshwater lens can also lead to stratification of the water column, which, when combined with exponential growth, reproduction, and decomposition of

phytoplankton due to an influx of nutrients, can lead to bottom water hypoxia when stratification is strong enough (Rabalais et al. 2002). Bottom hypoxia also alter community structure, as more motile organisms (e.g. adult fishes, shrimp) will evacuate the area, while less motile organisms (e.g. larval fishes, oysters) can experience physiological stress, or even perish, resulting in "dead zones"(Marcus 2001, Purcell et al. 2001, Breitburg 2002).

Larval fishes are generally more susceptible to environmental perturbations than adult stages, including habitat modifications as a result of freshwater discharge events. Temperature is likely the single-most important parameter determining larval fish survival (Brett 1979, Houde 1989). Temperature is positively correlated with larval fish growth rates, which in turn determines how long larvae remain in vulnerable life stages, as well as how quickly they will outgrow most of their potential predators (Houde 1989, McCormick and Molony 1995, Otterlei et al. 1999, Green and Fisher 2004). Similar to adults, changes in salinity may lead to shifts in abundances of larval fishes based on their salinity tolerances; however, most coastal species have a wide range of salinity tolerance (Christmas and Waller 1975, Peters and McMichael 1987, Barletta et al. 2005). Sediments that freshwater discharge carries into a marine environment can create turbid conditions, which may impact the feeding success of visually feeding larval fishes (Hunter 1981, Blaxter 1986). Presence of bottom-water hypoxia may lead to physiological stress in larvae which cannot escape to more tolerable oxygen levels, or shifts in vertical structure of planktonic (e.g. larvae, zooplankton) communities (Breitburg et al. 1999, Elliot et al. 2012). These freshwater-discharge related

environmental changes can have profound effects on larval fish survival, however, the effects are variable and difficult to predict.

The Consortium for Coastal River Dominated Ecosystems (CONCORE) was created to study the physical, chemical, and biological processes in the river-dominated northcentral GoM in order to better understand the potential impacts of future oil spills in the region (Greer et al. 2018). A major deliverable of CONCORDE is a 4D-synthesis model which incorporates field-collected data to characterize ecosystem processes and predict oil spill impacts (Greer et al. 2018). Within CONCORDE, my objective was to examine factors relevant to larval fish survival (e.g., diet, growth, condition) with respect to variability in the physical environment (e.g., temperature, salinity, turbidity, dissolved oxygen). For my thesis, I focused on two river-discharge related events sampled during CONCORDE: a unique, winter-time opening of a flood control structure in Louisiana, and a summer-time hypoxic event. The target taxa for my thesis were the ecologically important forage fish species Gulf Menhaden (*Brevoortia patronus*) and Atlantic Bumper (*Chloroscombrus chrysurus*). As adults, forage fishes form large schools that feed on phytoplankton and zooplankton, and are in turn fed upon by larger predators (Shaw and Drullinger 1990). As such, forage fishes play a critical role in marine ecosystem food webs. As fish larvae, they are potentially susceptible to environmental perturbations caused by river discharge, which may impact their survivorship.

CHAPTER II – VARIATION IN LARVAL GULF MENHADEN DIET, GROWTH, AND CONDITION DURING AN ATYPICAL, WINTER FRESHWATER DISCHARGE EVENT IN THE NORTHCENTRAL GULF OF MEXICO

2.1 Introduction

Many marine fisheries are associated with productive nearshore or estuarine environments, and are therefore heavily influenced by freshwater discharge which emanates from terrestrial sources (Sklar and Browder 1998). Sediment, pollutants, and nutrients interact with the marine environment, influencing the physical, chemical, and biological conditions of the nearshore region (Ryther and Dunstan 1971, Paerl et al. 2006). Freshwater discharge can alter habitat quantity and quality, trophic interactions, and the abundance and diversity of organisms within the riverine-influenced area (Justic et al. 1995, Conley 2000). Furthermore, fish populations have been shown to respond to the environmental variability associated with freshwater discharge. In general, fisheries production tends to increase with freshwater discharge, a result of overall productivity of a system increasing due to an abundance of nutrients (Sklar and Browder 1998, Grimes and Finucane 1991, Sanchez-Gil et al. 2008, Carassou et al. 2011).

Approximately 70-80% of all fisheries landings in the northern GoM occur within the Fertile Fisheries Crescent, a highly productive region off the coast of Louisiana, Mississippi, and Alabama with multiple sources of freshwater input (Gunter 1963, NMFS 1998). Populations of estuarine-dependent species such as Red Drum (*Sciaenops ocellatus*), Gulf Menhaden (*Brevoortia patronus*), King Mackerel (*Scomberomorus cavalla*), and Bluefish (*Pomatomus saltatrix*) are associated with freshwater discharge in the GoM (Grimes 2001) In general, as in other regions fisheries production in the

northern GoM is positively correlated with freshwater discharge. For example, Moore et al. (1970) found that catches of demersal species (e.g. *Micropogonias undulatus, Stenotomus caprinus, Cynoscion arenarius*) were highest in areas where discharge from the Mississippi River was greatest. Two species of flatfish in the GoM, Fringed Flounder (*Etropus crossotus*) and Bay Whiff (*Citharichthys spilopterus*), have been shown to exhibit peak recruitment during instances of higher freshwater discharge (Sánchez-Gil et al. 2008). Larval Engraulids, Sciaenids and Scombrids were all found in higher concentrations within river-discharge associated plume fronts in the GoM, which are hypothesized to provide richer food resources, leading to faster growth and higher survival of early life history stage fishes to adult stages (Grimes and Finucane 1991). Furthermore, juvenile American Kingfish (*Menticirrhus americanus*) abundances off Alabama have been shown to be positively correlated to freshwater discharge from Mobile Bay (Carrasou et al. 2011). However, not all freshwater discharge and fisheries relationships are positive. For example, in contrast to other studies, juvenile Atlantic Croaker recruitment (*M. undulatus*) was found to correlate negatively to Mobile Bay freshwater discharge (Carrasou et al. 2011). These studies suggest the effects of freshwater discharge can be stage-specific and species-specific, as well as variable between freshwater sources.

Estuarine-dependent species, such as the Gulf Menhaden, comprise a large percentage of the fisheries catch in the GoM (Houde and Rutherford 1993). The Gulf Menhaden fishery has consistently ranked among the largest fisheries in the GoM, bringing in hundreds of thousands of metric tons, and millions of dollars, to the Gulf coast annually (NMFS 2016). Adult Gulf Menhaden spawn in continental shelf waters

where currents facilitate the transport of eggs and larvae to estuarine habitats necessary for growth and development (Christmas et al. 1982, Shaw et al. 1985). It is essential for the early life stages to reach nearshore, nursey habitats in order to find food, suitable habitat, and protection from predators. Previous studies have reported mixed results with respect to Gulf Menhaden recruitment and freshwater discharge. Instances of increased annual freshwater discharge led to a reduction in subsequent yields of Gulf Menhaden, most likely due to larvae being pushed offshore by the expanding plume and away from nearshore nursery habitats (Deegan 1990, Govoni 1997). It has also been noted that "warm, wet" winters, accompanied by low salinity and high freshwater discharge, have led to poor recruitment of Gulf Menhaden (Guillory et al. 1983). However, Gulf Menhaden have also been shown to correlate positively to river discharge, likely due to riverine input leading to higher primary production, thus higher feeding incidences and faster growth (Govoni et al. 1989, Grimes and Finucane 1991), so the effects of freshwater influx are not clear or consistent.

On January 10th, 2016 the Bonnet Carré Spillway (BCS) in St. Charles Parish, Louisiana was opened for 23 days. The BCS is a river control structure built 33 river miles north of New Orleans, Louisiana to alleviate flooding in populated areas along the lower reaches of the Mississippi River. It is opened in cases of severe rainfall events and subsequent rises in flood stage (Brammer et al. 2007). When opened, a portion of water from the Mississippi River is diverted to Lake Pontchartrain where it then diffuses into the northern GoM through various inlets and channels, and delivers a pulse of nutrients and sediment into the Mississippi Bight, which runs roughly from the Mississippi River Delta to Apalachicola (Johnson and Perry 1999, Brammer et al. 2007). The 2016 opening

of the BCS was an especially unique event in that it was the first winter opening, and thus it overlapped with the Gulf Menhaden spawning season. Therefore, the opening of the BCS provided a unique opportunity to examine how freshwater from multiple sources, and the diversion of the Mississippi River, impacted the biotic and abiotic environment of larval Gulf Menhaden in the northern GoM.

The objectives for this chapter were to assess parameters related to survival of larval Gulf Menhaden in relation to abiotic and biotic environmental variability after the opening of the BCS. Fish early life stages are particularly susceptible to environmental variability; thus, it was expected that the conditions observed after the opening of the BCS would result in differences among larval Gulf Menhaden collected in different regions of the Mississippi Bight. Three distinct water masses were characterized, and larval Gulf Menhaden prey fields, diet, growth, and condition were compared among them.

2.2 Materials and Methods

2.2.1 Study Region

In response to the January 2016 opening of the BCS, the Consortium for Coastal River Dominated Ecosystems (CONCORDE) organized and led a research cruise aboard the R/V Point Sur (February 10-12, 2016) to examine BCS-related impacts on the biology, chemistry, and oceanography of the Mississippi Bight region. Samples were collected in several areas of the Mississippi Bight, including east of the Birdfoot Delta, south of Mobile Bay and west of the Chandeleur Islands (Figure 2.1). Environmental variability is common within the Mississippi Bight due in part to several freshwater sources such as the Mississippi River, Mobile Bay, Lake Pontchartrain, Lake Pearl, and

the Biloxi river systems (Sikora and Kjerfve 1985). During the BCS opening, Mississippi River water was partially diverted away from the Delta, through Lake Pontchartrain, where it then diffused into the Mississippi Sound. Over the course of 23 days, approximately 68,000 cubic meters of water was diverted through the BCS (US Army Corp of Engineers, n.d.).

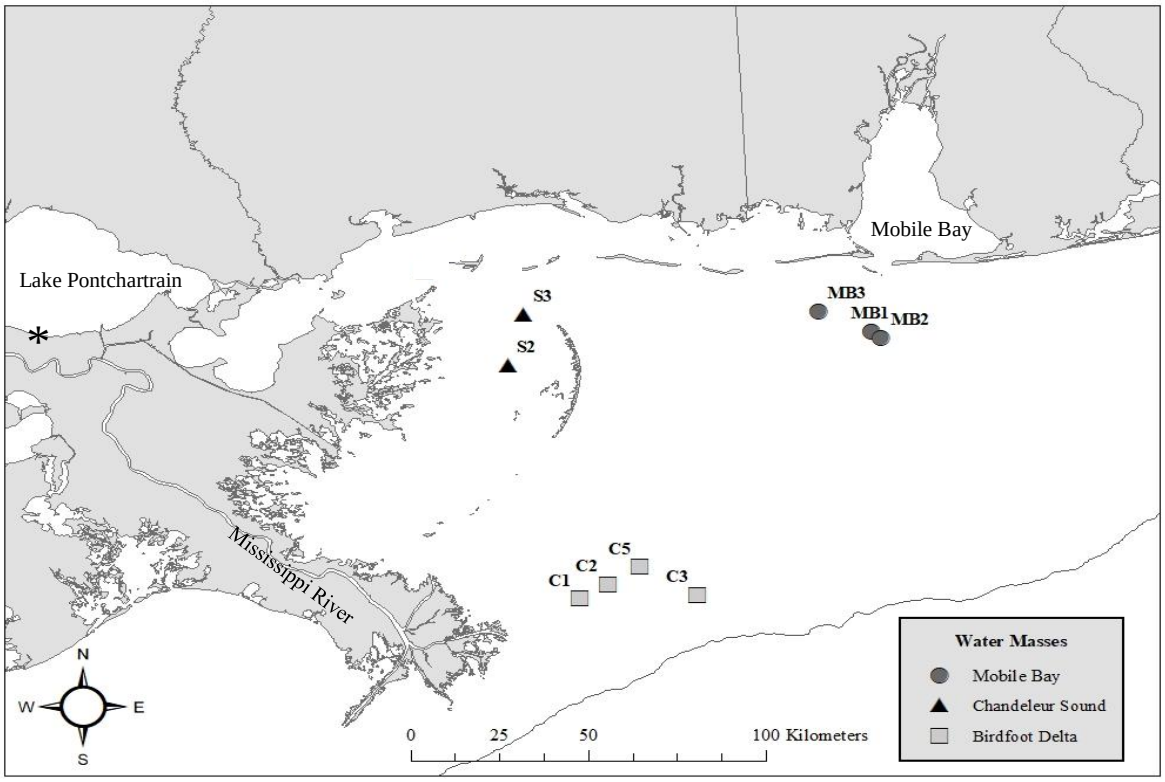

Figure 2.1 Locations of plankton sampling stations within the three different water masses (Mobile Bay, Chandeleur Sound, Birdfoot Delta) identified in the Mississippi Bight region of the northern Gulf of Mexico during the Bonnet Carre Spillway research cruise (February 10-12, 2016). The asterisk (*) denotes the location of the Bonnet Carre Spillway.

2.2.2 Water Mass Characterization

Three water masses were characterized by a suite of physical (temperature, salinity, light scattering) and biological (copepod abundance) parameters. Temperature and salinity profile data were collected using a Seabird Electronics Inc. 911 plus CTD and averaged for the upper 5 m of the water column. A WET Labs ac-s meter (towed at 2

m depth) was used to measure total spectral absorption and beam attenuation coefficients [$a_t(\lambda)$ and $c_t(\lambda)$, respectively] from 390-700 nm. To characterize the optical differences among water masses, the scattering coefficient [$b_t(\lambda)$, used as a proxy for turbidity] was calculated by subtracting absorption [$a_t(\lambda)$] values from attenuation [$c_t(\lambda)$] values at 530 nm (Twardowski et al. 2001). Univariate analyses (Kruskal-Wallis test, followed by a pairwise Wilcox test) were run for each physical (temperature, salinity, scattering coefficient) and biological (copepod abundance) parameter. Furthermore, the values for each parameter were then log-transformed and entered into a principal component analysis (PCA). The first two principal components were then compared among the three water masses using a Kruskal-Wallis test, followed by pairwise comparisons (significance tested at $\alpha = 0.05$).

2.2.3 Ichthyoplankton and Zooplankton Collection

Plankton samples were collected using a paired bongo net (60 cm) fitted with 202 µm and 335 µm mesh nets at sampling stations located within the Mobile Bay (n=3), Birdfoot Delta (n=4), and Chandeleur Islands (n=2) water masses. Bongo nets were towed just below the water surface for a duration of 10 minutes per tow. Mechanical flowmeters attached to the opening of each net were used to estimate the volume of water filtered. Samples were preserved in ethanol at sea. In the lab, each sample was sorted for larval fishes, of which Gulf Menhaden larvae were removed for further analyses. Gulf Menhaden abundances were standardized by filtered volumes to yield estimates of larval concentrations (number per cubic meter). Zooplankton were identified and enumerated from measured aliquots following the methods outlined in Harris et al. (2000).

Zooplankton abundances were standardized by aliquot and filtered volumes to yield estimates of taxon-specific concentrations (number per cubic meter).

2.2.4 Zooplankton Assemblage Analysis

To determine whether larval Gulf Menhaden prey availability differed among the three water masses, zooplankton assemblage structure was determined by a group-averaged, Hierarchical Cluster analysis using a Bray-Curtis similarity matrix. . A similarity profile (SIMPROF) was used to identify homogeneous groups based on zooplankton composition ($\alpha = 0.05$; 1000 permutations). Analysis of similarity (ANOSIM) was performed to test for significant differences in zooplankton composition among groups identified by Cluster analysis with SIMPROF. A Similarity Percentage (SIMPER) analysis was then used to identify the zooplankton taxa that accounts for most of the differences in assemblage structure among water masses.

2.2.5 Larval Gulf Menhaden Diet Analysis

Prior to dissection, larvae were imaged using a Canon EOS Rebel T3i digital camera system mounted onto Zeiss Stemi 2000-C dissecting microscope and measured to the nearest 0.1 mm (Ransom 2015). In order to account for ontogenetic dietary shifts, while maintaining sufficient sample sizes for each water mass, Gulf Menhaden between the range of 14-20 mm were retained for further analysis based on overall condition (i.e., with attached guts and heads). Fish with missing or empty guts were not included in the analysis. Diet analysis was performed following the protocols of Llopiz and Cowen (2008) and Carassou et al. (2009). For each larva, the entire alimentary canal was removed under a Leica MZ9.5 dissecting microscope, and gut contents were enumerated and identified when possible into prey categories. Differences in diet composition of

larval Gulf Menhaden among the three water masses were tested by Cluster and Multi-dimensional Scaling (MDS) analyses constructed using a Bray-Curtis similarity matrix in PRIMER.

Percent of total number (%N) of prey and percent frequency of occurrence (%FO) of prey items were calculated to further compare diet among the three water masses. In addition, Schoener's Index (1970) for diet overlap was calculated as:

$$\alpha = 100[\,1 - 0.5 \sum_{i=1}^{n} (P_{xi} - P_{yi})]$$

Where P_{xi} is the proportion of prey items in category *i* to total prey items for Gulf Menhaden in a water mass *x*, while P_{yi} represents the same proportion in a water mass *y*. The value of α ranges from 0 (no overlap) to 100 (complete overlap), with a value ≥ 60 is considered to be a biologically significant overlap in diet (Wallace 1981).

Calanoid copepods, the most common prey item, were imaged using the same camera system used for larval Gulf Menhaden measurements. The presome length of each calanoid copepod (to the nearest 0.1 mm) was measured as a proxy for prey size differences among the Chandeleur Sound (n=5), Birdfoot Delta (n=63), Mobile Bay (n=14) water masses and analyzed using a non-parametric Kruskal-Wallis test, followed by a pairwise Wilcox test. The abundance of calanoid copepods was also compared among the three water masses with a Kruskal-Wallis test, followed by a pairwise Wilcox test.

2.2.6 Larval Gulf Menhaden Growth Analysis

Larval Gulf Menhaden growth was estimated using otolith increment analysis. Sagittal otoliths were removed from each larva and mounted onto slides using

CrystalBond™ mounting adhesive. Otoliths were then imaged at 100x to 400x using a Canon EOS Rebel T3i digital camera system mounted onto an Olympus compound microscope (Ransom 2015). In order to minimize reader error, the longest possible radius was drawn on each otolith image prior to aging using iSolution light software, ensuring both readers would age and measure along the same axis. The left otolith was aged (unless damaged) independently by two different readers. If the two reads were not within 10% of each other, a third read was taken. If the third read was within 10% of one of the original reads, the otolith was used for further analysis; if it was not within 10% it was discarded (Sponaugle et al. 2005). Both readers then independently measured the width of the last two growth increments. Measurements were taken from the outside edge of a growth increment, to the outside edge of the subsequent increment (Pepin 2001). Measurements did not include the outer edge of the otolith, as it was not guaranteed to represent a full day's growth. Growth increment measurements followed the same 10% agreement protocol as aging. A random number generator determined which reader's measurements were used for analysis. The last two increments were averaged in order to assess the most recent growth, with the assumption that the fish had been entrained within the associated water mass for the last two days (Shulzitski et al. 2015). A Kruskal-Wallis test was used to test for differences in recent growth of larval Gulf Menhaden among the three water masses, and pairwise comparisons were performed to determine which water masses differed from one another.

2.2.7 Larval Gulf Menhaden Condition Analysis

Larval Gulf Menhaden body condition was estimated using Fulton's relative condition factor (K_n):

$$Kn = W/Wpred$$

where "W" is the measured weight of an individual larva and "W_{pred}" is the predicted weight based on the length-weight relationship. Individuals that had been previously imaged and measured (SL) were dried at 60°C for over 16 hours and weighed to the nearest 0.001 mg with a Mettler Toledo XP26 microbalance. A linear regression was then fitted to the observed lengths and dry weights to create a predicted weight for each length. Because data were non-normal, a Kruskal-Wallis test was used to compare median K_n values of larval fishes collected in each water mass; if differences were observed, a pairwise test was performed to determined which water masses differed from one another.

2.3 Results

2.3.1 Water Mass Characterization

Results from the Kruskal-Wallis tests, followed by pairwise comparisons for temperature ($H = 135.8$, $df = 2$, $p < 0.001$) (Figure 2.2) and salinity ($H = 87.8$, $df = 2$, $p < 0.001$) (Figure 2.2) revealed that each water mass differed significantly from one another. Temperature and salinity were significantly higher at the Birdfoot Delta stations, while the lowest temperature and salinity values were observed at the Chandeleur Sound stations. The Mobile Bay water mass was characterized as having intermediate conditions with respect to temperature and salinity (Figure 2.3). The scattering coefficient for each water mass was also significantly different among the water masses (Kruskal-Wallis test, $H = 63.7$, $df = 2$, $p < 0.001$), with the highest scattering (turbidity) at the Chandeleur

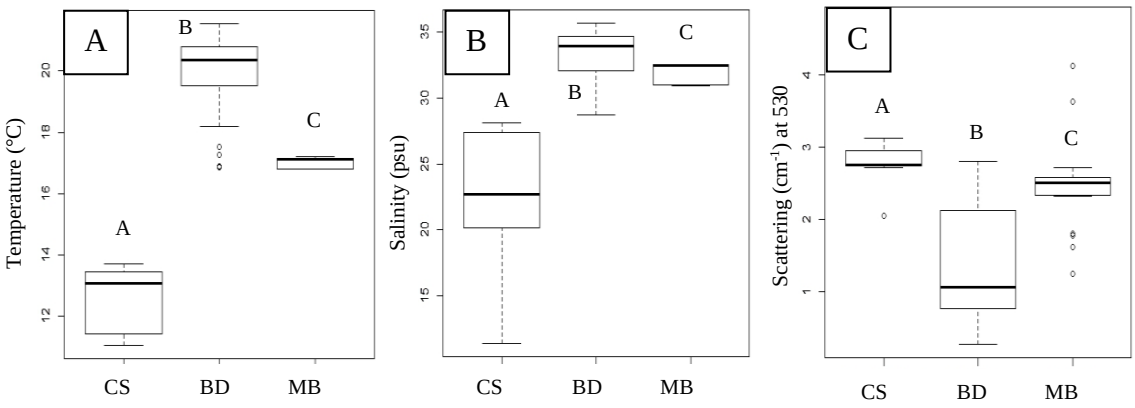

Figure 2.2 Boxplots of A) temperature, B) salinity, and C) scattering from the Chandeleur Sound (CS), Birdsfoot Delta (BD) and Mobile Bay (MB) sampling stations. The bold line within each box represents the sample median, and the upper and lower portion of each box represent the first and third quartiles. The ends of the "whiskers" (dashed lines) represent the minimum and maximum values. Letters indicate significance among water masses based on a Kruskal-Wallis test.

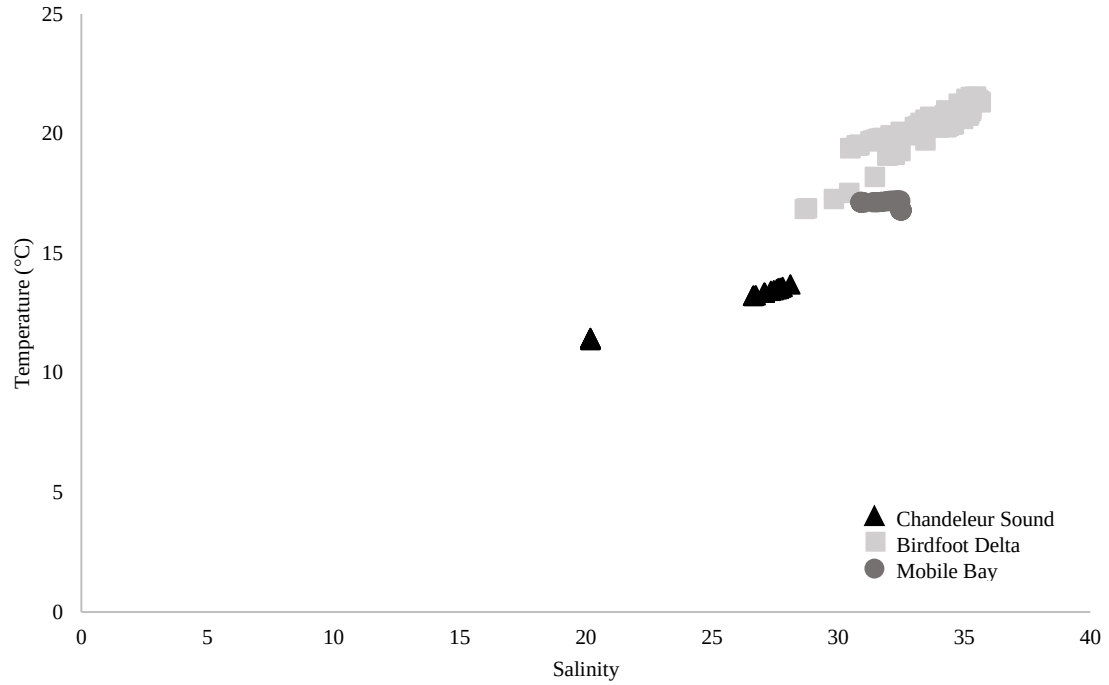

Figure 2.3 Temperature-Salinity plot based on CTD profile data (averaged for top 5 m of water column) collected within the Birdfoot Delta (squares), Mobile Bay (circles) and Chandeleur Sound (triangles) water masses during the BCS research cruise.

Sound stations and the lowest scattering at the Birdfoot Delta stations (Figure 2.2). The first component of the PCA (PC1) described the physical characteristics (temperature,

salinity, turbidity) of the water masses, and explained 64.3% of the variation observed (Figure 2.4). The results of the Kruskal-Wallis test were significant (H = 294.78, df = 2, p <0.001), and the following post hoc pairwise test revealed that each water mass differed significantly from one another based on their physical characteristics. The second component described the copepod abundance (available prey) and explained 31.3% of the observed variation (total = 95.6%) (Figure 2.4). The Kruskal-Wallis test revealed the same results (H = 221.8, df = 2, p <0.001), with each water mass differentiating significantly from the other two.

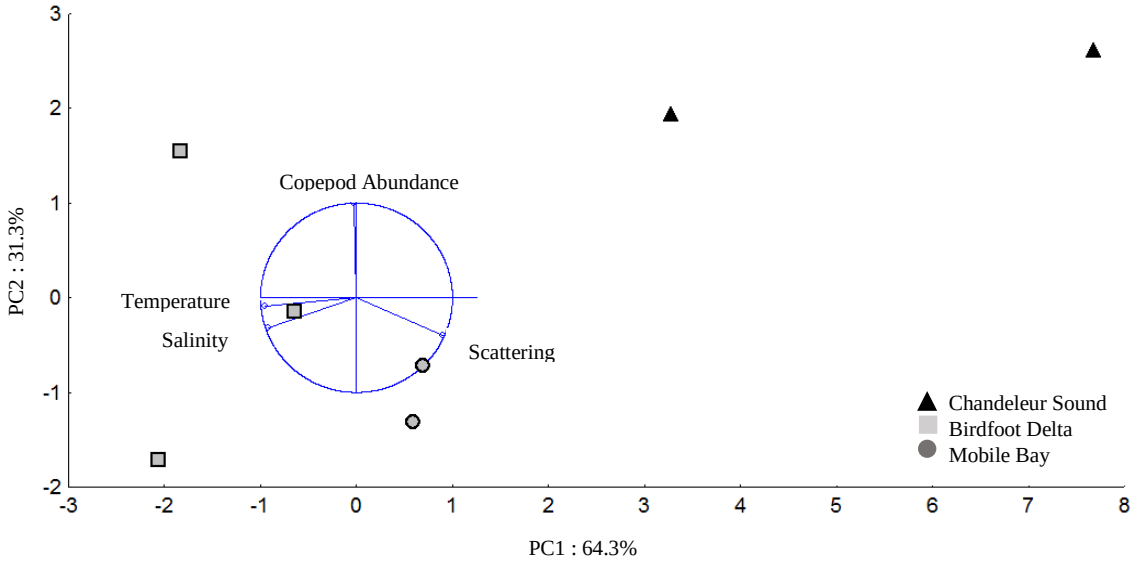

Figure 2.4 Results from a Principal Component Analysis of the explanatory variables (temperature, salinity, scattering, and copepod abundance) measured in the Birdfoot Delta (light gray squares), Chandeleur Sound (black triangles), and Mobile Bay (dark gray circles) water masses.

2.3.2 Ichthyoplankton and Zooplankton Collection

Larval Gulf Menhaden concentration did not differ significantly among the three water masses (Kruskal-Wallis test, H = 4.7, df = 2, p = 0.097) (Figure 2.5). Calanoid

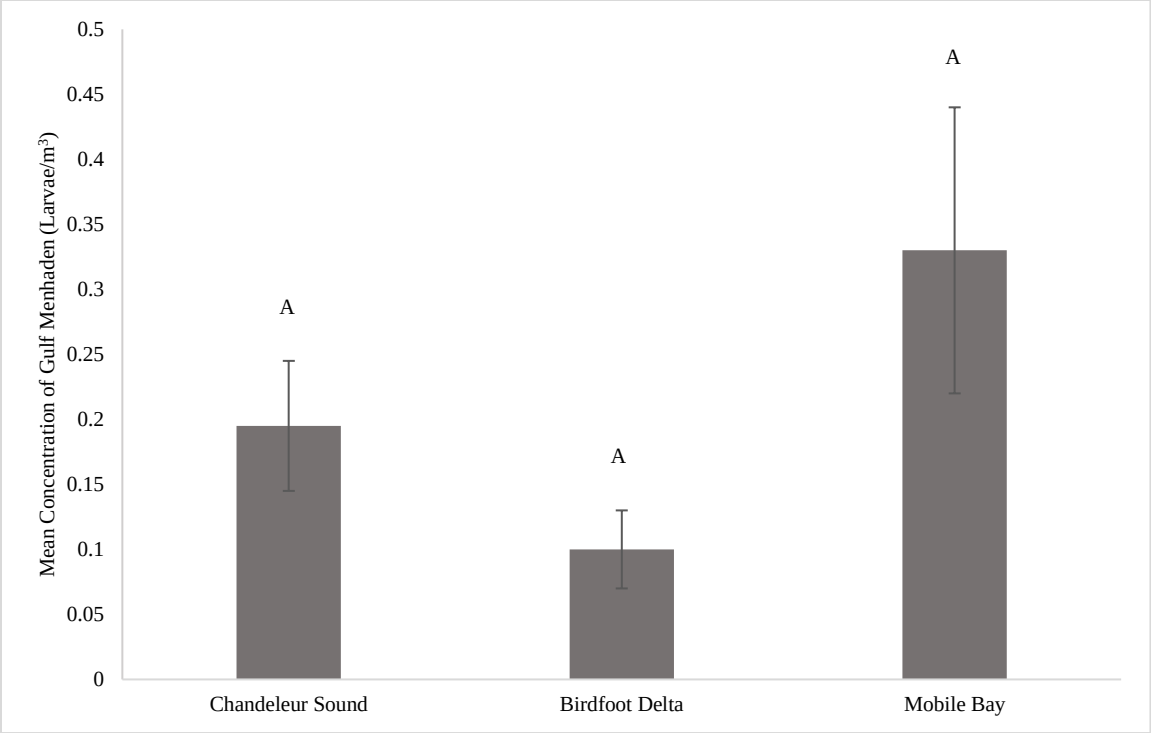

Figure 2.5 Mean concentration (larvae/ m^3) of Gulf Menhaden larvae collected at sampling stations within the Chandeleur Sound, Birdfoot Delta, and Mobile Bay water masses. Error bars represent standard error. Letters indicate significance among water masses based on a Kruskal-Wallis test.

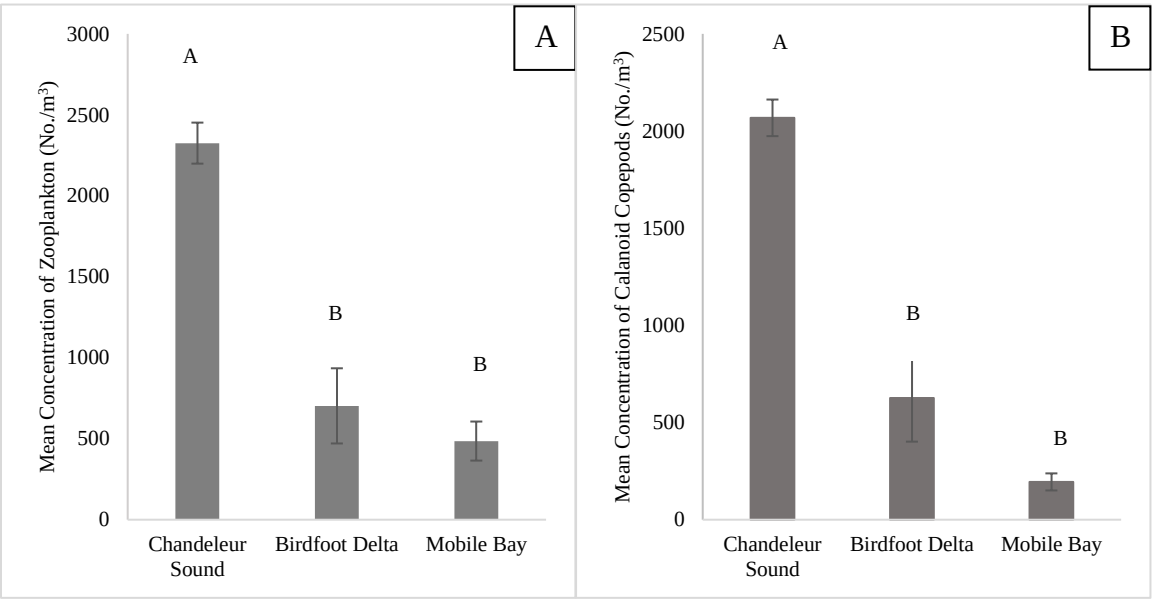

Figure 2.6 Mean concentration (No./m^3) of A) total zooplankton and B) calanoid copepods collected at sampling stations within the Chandeleur Sound, Birdfoot Delta, and Mobile Bay water masses. Error bars represent standard error. Letters indicate significant differences among water masses based on a Kruskal-Wallis test.

copepods, cyclopoid copepods, copepod nauplii, chaetognaths, larvaceans, barnacle nauplii, and unidentified decapods were the dominant zooplankton groups, and were collected in at least 50% of the samples in this study. Total zooplankton concentration was significantly higher in the Chandeleur Sound water mass relative to the Birdfoot Delta and Mobile Bay water masses (Kruskal-Wallis test, $H = 8.88$, $df = 2$, $p = 0.012$) (Figure 2.6). Calanoid copepod concentration was also significantly different among the water masses, with the highest concentration in the Chandeleur Sound (Kruskal-Wallis test, $H = 9.43$, $df = 2$, $p = 0.009$) (Figure 2.6). Of the larval Gulf Menhaden collected during the cruise, 292 larvae met the criteria for further analyses (Table 2.1), although relatively few (n=24) were collected in the Chandeleur Sound water mass.

Table 2.1 Sample sizes, mean density, mean standard length, and size ranges for larval Gulf Menhaden collected at sampling stations within three water masses in the Mississippi Bight. Standard Error (SE) is reported in parentheses.

	Water Mass		
	Chandeleur Sound	Birdfoot Delta	Mobile Bay
No. of Net Samples	4	8	6
Total No. Gulf Menhaden Larvae	104	179	395
Mean Gulf Menhaden Concentration, no./m^3 (SE)	0.195 (0.05)	0.10 (0.03)	0.33 (0.11)
Total No. Gulf Menhaden, 14-20mm	24	152	118
Mean Standard Length, mm (SE)	15.3 (0.2)	17.0 (0.1)	17.9 (0.1)
Standard Length Range, mm	14.1-17.1	14.2-19.8	14.8-20

2.3.3 Zooplankton Assemblage

Four distinct zooplankton assemblages were identified by a Cluster analysis using SIMPROF (Figure 2.7). ANOSIM revealed that each cluster was significantly different from each other ($R^2 = 0.474$, $p = 0.001$) based on differences in zooplankton composition. One of the clusters was comprised of samples from one station of the Chandeleur Sound region (S2). Another cluster included two stations from the Mobile Bay region (MB1 and MB2). A third cluster included two stations from the Birdfoot Delta region (C2 and C1). The fourth cluster included a mixture of the remaining stations from each of the three water mass (S3, C3, C5, and MB3). A SIMPER analysis revealed that the abundances of calanoid copepods, cladocerans, cyclopoid copepods, crab zoea and other decapods were among the taxa which contributed the greatest percentage of dissimilarity among the three water masses (Table 2.2).

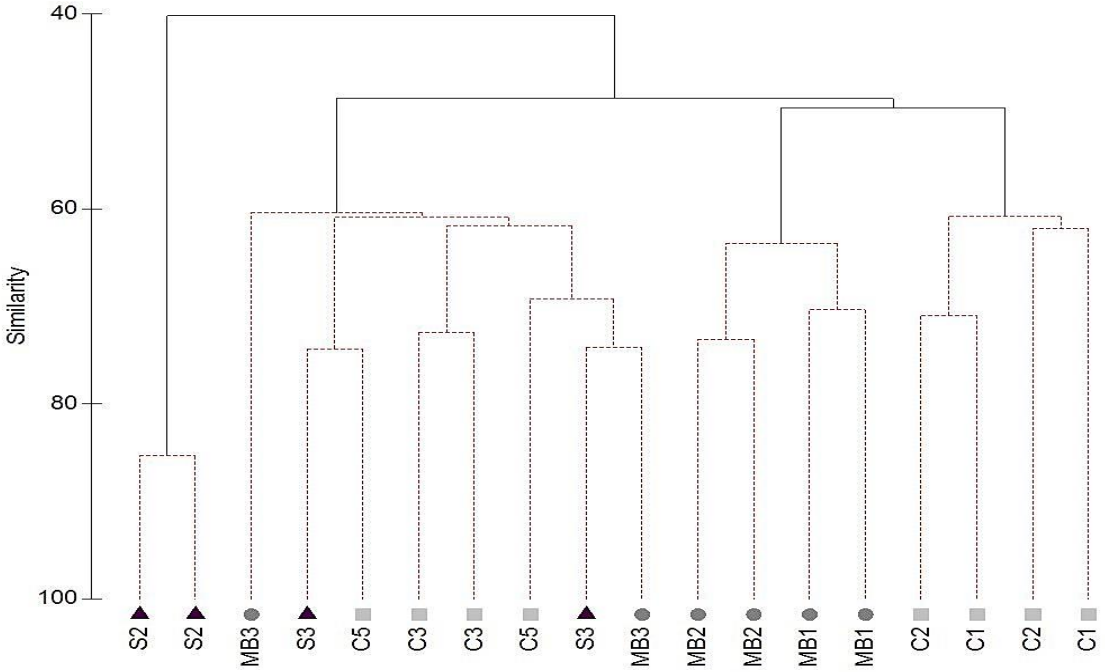

Figure 2.7 Results of a Cluster analysis for zooplankton collected within the Mobile Bay (circles), Birdfoot Delta (squares) and Chandeleur Sound (triangles) water masses identified during the Bonnet Carré Spillway cruise in February 2016. Four clusters are shown via the dotted brackets, which indicate homogeneity.

Table 2.2 Results from a SIMPER analysis of zooplankton abundances among water masses. Av. Abund CS = Average Abundance from Chandeleur Sound; Av. Abund BD = Average Abundance from Birdfoot Delta; Av. Abund MB= Average Abundance from Mobile Bay; Av. Diss. = Average Dissimilarity; % Cum. = Cumulative Percentage of Dissimilarity.

Species	Av. Abund. CS	Av. Abund. BD	Av. Abund. MB	Av. Diss.	% Cum.
Chandeleur Sound & Birdfoot Delta Av. Dissimilarity: 62.76%					
Calanoid Copepod	1831.9	626.2	-	54.3	86.5
Cladoceran	126.3	0.0	-	4.2	93.2
Chandeleur Sound & Mobile Bay Av. Dissimilarity: 79.53%					
Calanoid Copepod	1831.9	-	194.4	61.2	76.9
Crab Zoea	0.0	-	97.4	4.6	82.7
Cladoceran	126.3	-	2.0	4.3	88.2
Cyclopoid Copepod	12.7	-	51.0	2.7	91.5
Birdfoot Delta & Mobile Bay Av. Dissimilarity: 67.66%					
Calanoid Copepod	-	629.2	194.4	37.7	55.7
Crab Zoea	-	0.0	97.4	9.5	69.7
Other Decapod	-	30.5	56.4	5.7	78.2
Cyclopoid Copepod	-	11.1	51.0	5.7	86.5
Copepod Nauplii	-	5.6	21.9	1.9	89.3
Larvacean	-	8.2	10.2	1.5	91.5

2.3.4 Larval Gulf Menhaden Diet

A total of 292 larvae were examined for gut contents, of which 115 larvae (39%) contained prey items. Most of the larvae examined from the Mobile Bay water mass had empty guts (80%), followed by larvae from the Chandeleur Sound (59%) and the Birdfoot Delta (46%) water masses. A total of 272 prey items were identified, of which approximately 82% were calanoid copepods (n=222). Results from the Cluster and MDS

analysis suggested larval Gulf Menhaden diets did not differ among the three water masses (Figure 2.8). The number of prey items per larva was significantly less for larval Gulf Menhaden in the Mobile Bay water mass than for the larvae in the Birdfoot Delta or Chandeleur Sound water masses (Kruskal-Wallis test, $H = 46.22$, $df = 2$, $p < 0.001$) (Figure 2.9).

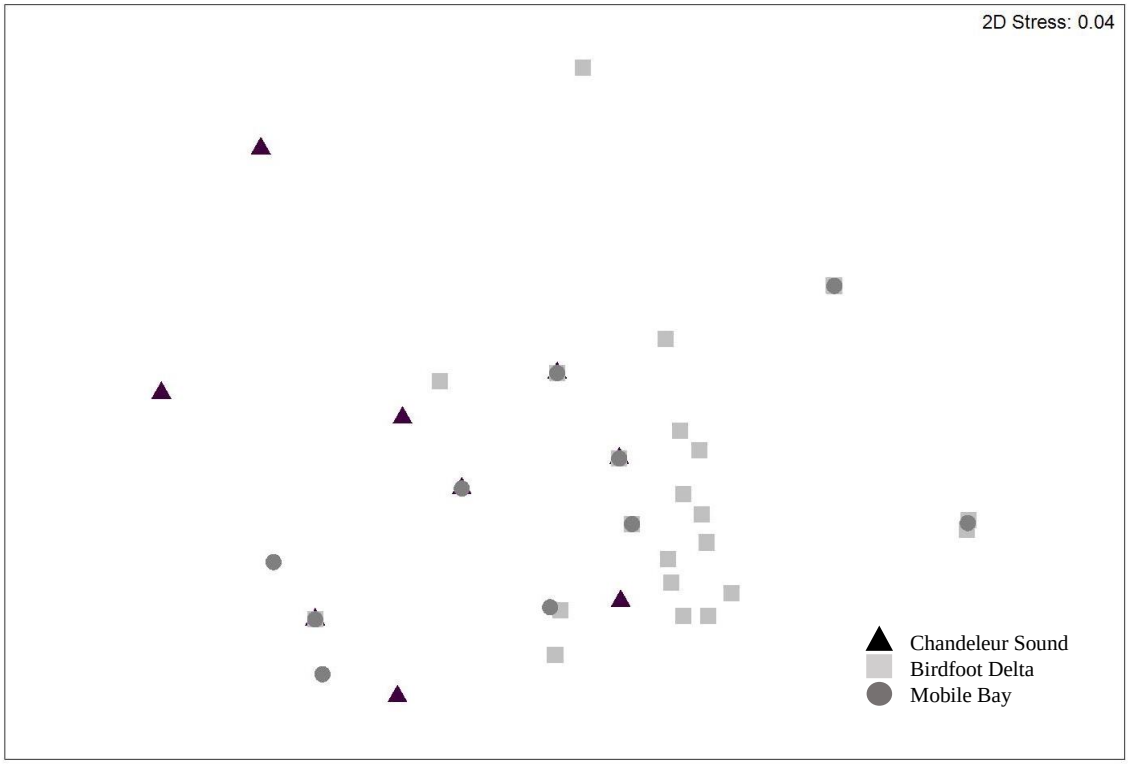

Figure 2.8 Results of a multi-dimensional scaling analysis for the diet of each larval Gulf Menhaden containing prey collected within the Chandeleur Sound (triangles), Birdfoot Delta (squares), and Mobile Bay (circles) water masses identified during the Bonnet Carré Spillway cruise in February 2016. Each symbol represents an individual larva.

Calanoid copepods were the dominant prey item in all three water masses (Figure 2.10). The %N of calanoid copepods was at least 50% in all three water masses, with the Birdfoot Delta having the greatest at 87.9%, Mobile Bay larvae having a %N of 63.2%, and the Chandeleur Sound water mass %N at 50%. The %FO of calanoid copepods was greatest in the Birdfoot Delta water mass (49.0%), followed by Chandeleur Sound (20.8%), then the Mobile Bay water mass (9.9%) (Table 2.3). A non-parametric Kruskal-

Wallis test (H = 17.8, df = 2, $p < 0.001$) followed by a pairwise comparisons, suggested that the sizes of calanoid copepods (presome length, mm) in the Chandeleur Sound and Mobile Bay water masses were significantly smaller than in the Birdfoot Delta water mass (Figure 2.9). The calculated Schoener's Index value was greatest between the Chandeleur Sound and Mobile Bay water masses (80.2), indicating a significant overlap (i.e. greater than 60) and lowest between the Chandeleur Sound and Birdfoot Delta water masses (54.3), indicating a marginally different diet (Table 2.4).

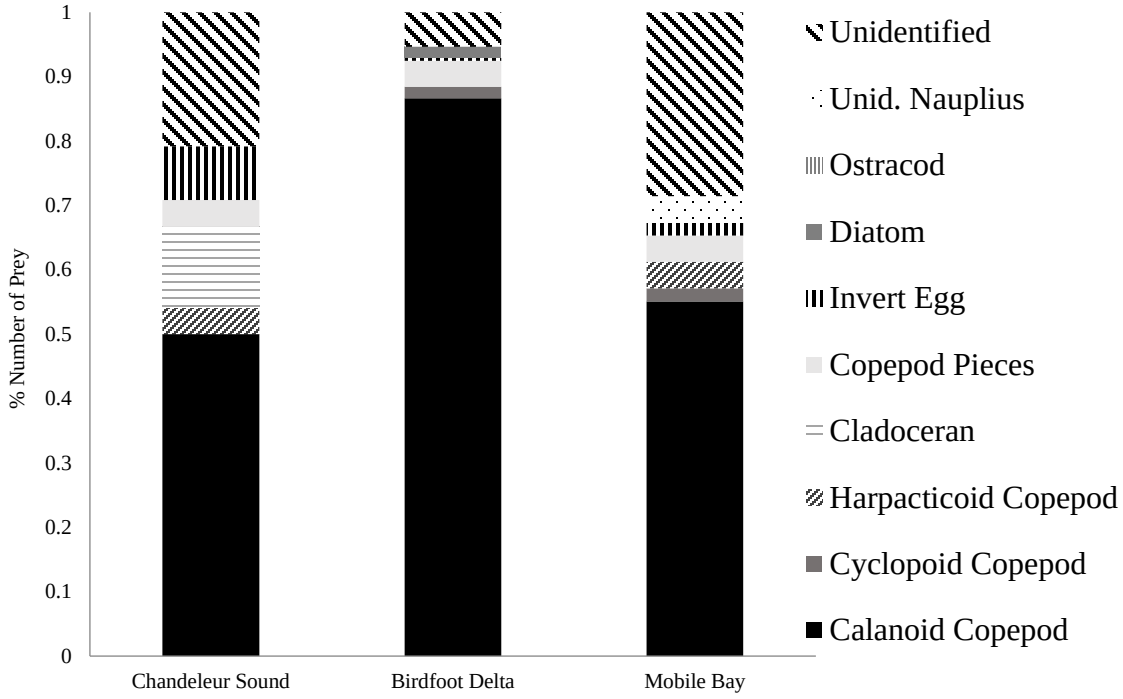

Figure 2.9 Percentages of identified prey in the guts of Gulf Menhaden larvae from the Chandeleur Sound, Birdsfoot Delta and Mobile Bay sampling stations.

Table 2.3 Gut content analysis of 127 larval Gulf Menhaden. %N = percent of the total prey items (N) found in that water mass: FO = frequency of occurrence; %FO = percent frequency of occurrence among larvae containing food; n = the total number in each category.

	Water Masses											
	Chandeleur Sound				Birdfoot Delta				Mobile Bay			
Prey Item	n	%N	FO	%FO	n	%N	FO	%FO	n	%N	FO	%FO
Calanoid Copepod	10	50.0	5	20.8	188	87.9	76	49.0	24	63.2	16	9.9
Cyclopoid Copepod	-	-	-	-	4	1.9	4	2.6	-	-	-	-
Harpacticoid Copepod	1	5.0	1	4.2	-	-	-	-	2	5.3	2	1.2
Cladoceran	3	15.0	2	8.3	-	-	-	-	-	-	-	-
Copepod Pieces	-	-	-	-	9	4.2	9	5.8	1	2.6	1	0.6
Invert Egg	1	5.0	1	4.2	1	0.5	1	0.6	1	2.6	1	0.6
Diatom	-	-	-	-	3	1.4	2	1.3	-	-	-	-
Ostracod	-	-	-	-	-	-	-	-	-	-	-	-
Unid. Nauplius	-	-	-	-	-	-	-	-	1	2.6	1	0.6
Unidentified	5	25.0	4	16.7	9	4.2	3	1.9	9	23.7	8	4.9
Total Prey	20				214				38			
No. of Fish	22				152				116			
No. of Empty Guts	13				70				92			

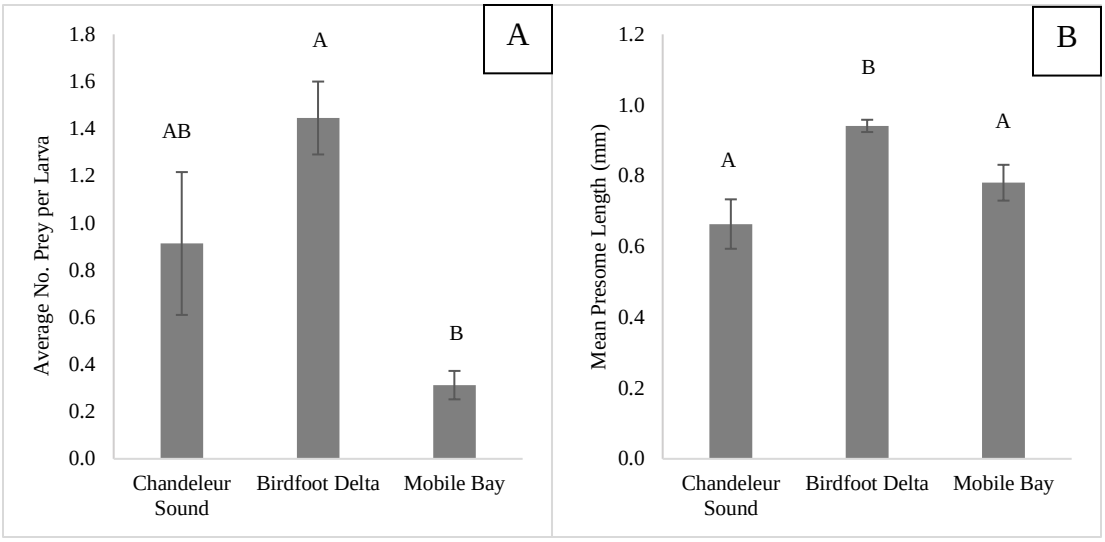

Figure 2.10 A) Mean number of prey found in the guts of larval Gulf Menhaden collected at stations within the three water masses sampled in February 2016. B) Mean size (presome length, mm) of calanoid copepods (most common prey item) found in the guts of Gulf Menhaden larvae collected at sampling stations within the three different water masses. Error bars represent standard error. Letters indicate significant differences among water masses based on a Kruskal-Wallis test.

Table 2.4 Matrix of Schoener's Index values (diet overlap) for larval Gulf Menhaden diet among water masses.

	Schoener's Index Values	
	Chandeleur Sound	Birdfoot Delta
Birdfoot Delta	54.3	-
Mobile Bay	80.2	69.2

2.3.5 Larval Gulf Menhaden Growth

Recent growth (average of the last two growth increments) was determined for 55 larvae which met the analysis criteria. Results from a Kruskal-Wallis test indicated that the recent growth of larval Gulf Menhaden differed among water masses ($H = 25.6742$, $df = 2$, $p < 0.0001$) (Figure 2.11). Post hoc pairwise comparisons determined the recent growth of larvae from the Chandeleur Sound water mass (n=12) was significantly lower

than that of larvae collected in the Mobile Bay (n=11) or Birdfoot Delta (n=32) water masses.

2.3.6 Larval Gulf Menhaden Condition

A total of 292 larval Gulf Menhaden met the criteria for estimating K_n and were used to compare relative condition among water masses. Results from Kruskal-Wallis tests suggested that relative condition differed among the water masses ($H = 78.35$, $df = 2$ $p < 0.0001$) (Figure 2.11). Larvae collected in the Chandeleur Sound (n=23) and Mobile Bay (n=117) water masses were in poorer condition than larvae collected in the Birdfoot Delta water mass (n=153).

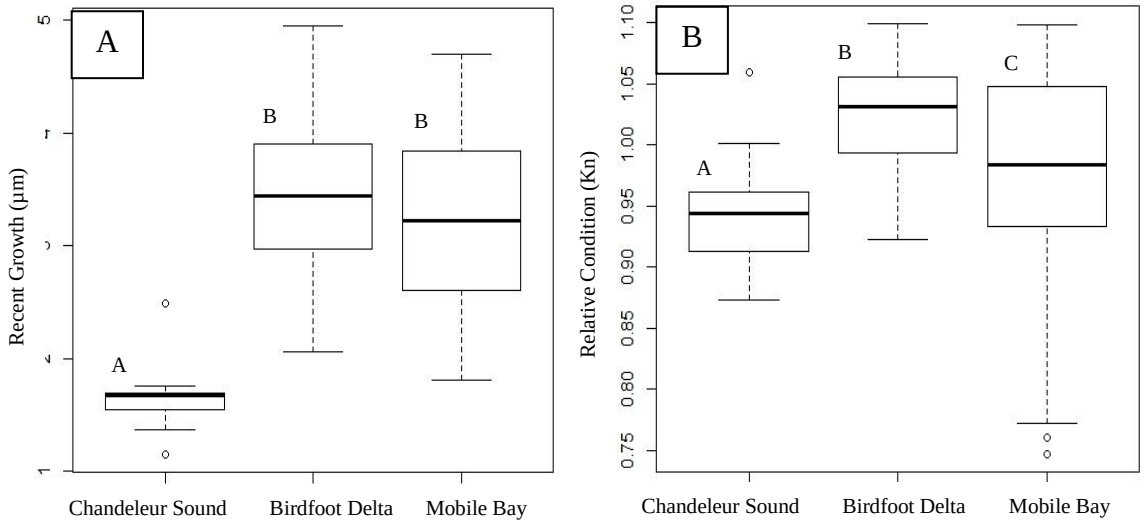

Figure 2.11 A) Boxplots of recent larval growth between larvae collected from the Chandeleur Sound (n = 12), Birdfoot Delta (n=32), and Mobile Bay (n=11) sampling regions in February 2016. B) Boxplots of relative condition factor (K_n) for Gulf Menhaden larvae collected from the Chandeleur Sound (n=23), Birdfoot Delta (n=153), and Mobile Bay (n=117). The bold line within each box represents the sample median, and the upper and lower portion of each box represent the first and third quartiles. The ends of the "whiskers" (dashed lines) represent the minimum and maximum values. Open circles outside of the whiskers are outliers. Letters indicate significant differences among water masses based on a Kruskal-Wallis test.

2.4 Discussion

The unprecedented 2016 winter opening of the BCS, combined with increased freshwater discharge from other sources (e.g., Mobile Bay), resulted in highly variable hydrographic and environmental conditions within the Mississippi Bight. Clupeids are particularly sensitive to environmental influences during early life stages (Cushing 1969, Ahrenholz 1991), and my study suggests that the observed variability in environmental conditions coincided with variable growth and condition of larval Gulf Menhaden collected from distinct water masses (Table 2.5). Specifically, larvae collected in the Chandeleur Sound water mass exhibited relatively lower recent growth, and were in poorer condition than those collected in the Birdfoot Delta and Mobile Bay water masses. Further, my results suggest that several of the observed physical and biological parameters may have contributed to the variability in larval Gulf Menhaden growth and condition. Notably, the Chandeleur Sound water mass was characterized by significantly lower water temperature and salinity, as well as higher turbidity, factors that have previously been identified as contributing to slow growth and poor body condition in larval fishes.

Previous research has identified temperature as the dominant factor in determining larval fish growth, with higher temperatures leading to faster growth (Houde 1989, Green and Fisher 2004). For example, Durieux et al. (2009) reported positive relationships between temperature and the size and growth rate of larval Silver-stripe Round Herring (*Spratelloides gracilis*), a clupeid common to the waters of Western Australia. Similarly, ontogenetic changes of several species of fishes, including several species of flatfishes and Atlantic Menhaden, have been shown to occur sooner at warmer

temperatures (Crawford 1984, Fuiman et al. 1998, Chambers and Leggett 2011). Gulf Menhaden larvae have been collected in a wide range of temperatures, with an optimum range between 15-25°C (Christmas et al. 1982). The average temperature of the Chandeleur Sound (12.4 °C) water mass at the time of collection was below this range, and significantly lower than the Birdfoot Delta (20.1 °C) and Mobile Bay (17.0 °C) water masses. Lower than optimal temperatures in the Chandeleur Sound water mass likely contributed to the slower growth rates seen in this water mass relative to the Birdfoot Delta and Mobile Bay water masses.

Table 2.5 Summary of statistical comparisons among sampling locations in three different water masses for larval fish parameters (growth, condition) and the explanatory variables examined in this study (temperature, salinity, scattering, prey concentration, number of prey per larva, and prey size). Statistical treatments for each set of comparisons are described in the Methods section. A greater than sign (>) between any two location pairs indicates a significantly higher value was detected for the factor or variable; a lesser than sign (<) denotes a significantly lower value detected between the pairing; and an equal sign (=) denotes no significant difference between the pairing.

	Statistical Relationships				
Larval Factors					
Growth	Birdfoot Delta	=	Mobile Bay	>	Chandeleur Sound
Condition	Birdfoot Delta	>	Mobile Bay	>	Chandeleur Sound
Explanatory Variables					
Temperature	Birdfoot Delta	>	Mobile Bay	>	Chandeleur Sound
Salinity	Birdfoot Delta	>	Mobile Bay	>	Chandeleur Sound
Particle Scattering	Birdfoot Delta	<	Mobile Bay	<	Chandeleur Sound
Copepod Abundance	Birdfoot Delta	=	Mobile Bay	<	Chandeleur Sound
No. Prey per Larva	Birdfoot Delta	=	Chandeleur Sound	>	Mobile Bay
% Empty Guts	Birdfoot Delta	<	Chandeleur Sound	<	Mobile Bay
Prey Size	Birdfoot Delta	>	Mobile Bay	=	Chandeleur Sound

In addition to having the lowest mean temperature among the water masses, the mean salinity of the Chandeleur Sound (21.9) water mass was significantly lower than that of the Birdfoot Delta (33.3) and Mobile Bay (32.0) water masses. Larval Gulf Menhaden have been collected over a wide range of salinity (6-36), but are more often collected in higher salinity waters (>25) (Christmas and Waller 1975). Shaw et al. (1985), for example, reported the highest densities of larval Gulf Menhaden off Louisiana were collected in a salinity range of 29-36 psu. Many fish species have optimal ranges of salinity for growth and development (Tandler et al. 1995, Smith et al. 1999, Boeuf and Payan 2001), but little is known about salinity optima for larval Gulf Menhaden. Because larval Gulf Menhaden are euryhaline, it is difficult to discern whether the lower salinity in the Chandeleur Sound water mass (which was still within their reported salinity range) contributed to the relatively slow growth rates, or poorer body condition observed in this region.

The influx of cooler, less saline water from various local sources, as well as the BCS, resulted in a turbid water column, particularly in the Chandeleur Sound water mass, where the observed water column scattering (proxy for turbidity) was significantly higher than in the Birdfoot Delta and Mobile Bay water masses. Larval fishes are highly dependent on vision for feeding (Hunter 1981, Blaxter 1986), and larvae in water with a high number of particulates would therefore be expected to experience lower feeding efficiency due to decreased visibility (Sirois and Dodson 2000, Utne-Palm 2001, Robertis et al. 2003). The abundance of copepods (the most dominant prey type in this study) was significantly higher in the Chandeleur Sound water mass, which would suggest that prey availability should not be limiting, and that the larvae from the Chandeleur Sound should

have more prey in their gut, as a higher density of preferred prey was available to them. However, the mean number of prey per larva (0.91) and proportion of guts with prey (41%) were lower in larvae collected in the Chandeleur Sound water mass than in those collected in the Birdfoot Delta water mass (1.4 prey per larva; 54% with prey), where larval growth and condition were significantly higher. This suggests that the higher number of particles in the water may have obstructed their ability to locate and capture prey.

Biotic factors, including the quantity and quality of available prey, influence growth and survival of larval fishes (Hunter 1981). The prey available to the larval fishes is important because diet heavily influences condition and is highly correlated to growth (Pepin et al. 2015). Although the zooplankton communities observed at individual stations within each water mass often clustered together, another subset of stations from each water mass comprised a fourth cluster, making the groupings difficult to interpret. A SIMPER analysis of the clusters revealed that the abundance of calanoid copepods was the primary driver of dissimilarity of zooplankton community structure observed among the water masses. Calanoid copepods are generally abundant in the northern GoM and are an important prey item for many species of fishes (Govoni et al. 1983, Baier and Purcell 1997), including Gulf Menhaden. Although the abundance of calanoid copepods was significantly higher in the Chandeleur Sound water mass than in the other regions, they were still the most abundant zooplankton taxa in all three water masses. In this study, the diets of the larval Gulf Menhaden were not significantly different among the three water masses. Because copepods are a preferred prey item, it is to be expected that the larval fish diets would be similar among the water masses if copepods were present in high

abundances (June and Carlson 1971, Stoecker and Govoni 1984, Deegan et al. 1990). When considering the results of the zooplankton analyses, it should be noted that the taxonomic resolution used was relatively coarse, and that narrowing down the taxonomic resolution and stage of the zooplankton may result in more detailed structuring of the community composition and foraging ecology of larval fishes.

The results of this study suggest that the environmental variability created in occasions of heavy rainfall can influence parameters important to potential survival of fisheries-important species such as the Gulf Menhaden. While the environmental variability observed coincided with variable larval Gulf Menhaden condition and growth, this study is a snapshot of the possible conditions larvae may be exposed to in their early life stages. Baseline data are needed to determine where these results fall within the natural variability of larval Gulf Menhaden diet, growth, and condition. If climatic conditions continue to get more extreme as is predicted (Justic et al. 1996) levels of rainfall may become more drastic and persistent, increasing freshwater runoff, as well as nutrient and particulate input, intensifying the results seen in this study by severely impeding the ability of larvae to ingress, feed, and survive to adult populations. The ability of early life stages to recruit to adult populations is a major contributor to year-class strength, therefore, accounting for the variability seen in larval fish survival parameters related to the spatial environmental variability, as seen in this study, in stock assessment models may provide more accurate predictions of population sizes. Furthermore, these data can be incorporated into the 4D synthesis model of CONCORDE in terms of larval fish growth rates in relation to environmental parameters (temperature, salinity), which can also be used for future coastal management assessments.

CHAPTER III – DIET, GROWTH, AND CONDITION OF LARVAL ATLANTIC BUMPER UNDER NORMOXIC AND HYPOXIC CONDITIONS IN THE NORTHCENTRAL GULF OF MEXICO

3.1 Introduction

Hypoxic (low oxygen) conditions in near-bottom marine waters occur globally in coastal environments, often through natural processes. However, some hypoxic regions are formed or exacerbated by human activity, and are spreading and expanding in size (Diaz and Rosenburg 1995). The northern GoM, for example, experiences the largest hypoxic region in the western hemisphere, and the second largest in the world annually (Rabalais et al. 2002, Kimmel et al. 2009, Bianchi et al. 2010). Hypoxia has long been present in the GoM, however the extent and duration of hypoxia have been increasing as nitrogen inputs from the Mississippi River have nearly tripled since the 1950's (Turner and Rabalais 1994). This "Dead Zone" off the coast of Louisiana forms annually via several co-occurring processes. Increased freshwater runoff during the spring (mostly from the Mississippi River drainage basin) delivers excess nutrients (nitrogen, phosphorus) from terrigenous sources (e.g., agriculture, industry) to the marine environment, allowing phytoplankton to grow and reproduce at an exponential rate (Bianchi et al. 2010). The influx of freshwater also facilitates the formation of a stratified water column with a relatively low density freshwater lens overlaying a higher density seawater layer (Rabalais et al. 2002). As the excess nutrients are depleted in the upper water column, phytoplankton carcasses sink to the bottom where bacterial decomposition consumes oxygen, which cannot be replaced due to intense thermal stratification of the

water column, resulting in oxygen-depleted, near-bottom waters (Rabalais et al. 2002, Diaz and Rosenburg 2008, Bianchi et al. 2010).

The large hypoxic region off the coast of Louisiana is an annual occurrence, and it is highly variable in size, duration, and intensity (Elliot et al. 2012, Obenour et al. 2013). Other coastal and shelf regions of the northern GoM experience hypoxic conditions as well, though not at the same scale (Turner et al. 1987). Brunner et al. (2006) illustrated how hypoxia is common throughout the Mississippi Bight, occurring along the barrier islands off Mississippi, the continental shelf east of the Mississippi River Delta, and within the Chandeleur Islands. Furthermore, hypoxia is a common occurrence within Mobile Bay, as well as the shelf waters south of Mobile Bay (eastern Mississippi Bight) (Park et al. 2007). Overall, the northern GoM is a complex hydrographic environment which experiences seasonal circulation, wind-mixing, storms, freshwater discharge plumes, and intense stratification, making it difficult to predict where other localized hypoxic zones will occur.

Hypoxia in marine environments has been shown to negatively impact marine organisms. When exposed to low levels of oxygen, highly motile organisms such as fishes and shrimp may leave the area, while less motile organisms (e.g. oysters, larval fishes) may experience physiological stress, trophic shifts, reduction in growth or reproduction, or even perish (Rabalais et al. 2001, Breitburg 2002). For example, Bell and Eggleston (2005) reported lower densities of (mostly demersal) fishes (e.g., *Micropogonias undulatus, Leiostomus xanthurus, Lagodon rhomboides, Paralichthys dentatus*) and blue crab (*Callinectes sapidus*) when hypoxia was present in the Neuse River estuary (North Carolina). Similarly, on the GoM shelf, Craig and Crowder (2005)

reported offshore displacement of Atlantic Croaker (*M. undulatus*) and inshore displacement of Brown Shrimp (*Farfantepenaeus aztecus*) in response to hypoxia, and suggested that such movements of these demersal species had implications for trophic interactions and energy utilization. Displacement of a pelagic species, the Atlantic Bumper (*Chloroscombrus chrysurus*), has also been observed (Hazen et al. 2009), though the effect was less pronounced, which suggests that the magnitude of response may be species-specific due to physiological tolerances, and related to its position in the water column.

Although hypoxic waters are operationally defined as having levels of dissolved oxygen < 2 mg/l, larval fishes have shown signs of stress, avoidance, and mortality at dissolved oxygen levels higher than this threshold (Secor and Gunderson 1998, Breitburg 2002). Unlike adult fishes with more capable swimming abilities, low levels of dissolved oxygen can particularly affect larval stages of fishes, which may be unable to migrate away from hypoxic waters (Rabalais et al. 2002). Low dissolved oxygen levels can also alter the distribution, abundance, and composition of zooplankton prey (Elliot et al. 2012). For example, in the GoM copepods found within the hypoxic layer of the water column have been shown to be larger than those in normoxic water, altering the quality of prey available to larval fishes (Kimmel et al. 2009, Kimmel et al. 2010). Other studies have shown that some zooplankton can utilize hypoxic zones as refuges from predation (Zhang et al. 2009, Elliot et al. 2012). Hypoxia-induced changes in zooplankton availability may have profound effects on fish larvae, which begin feeding exogenously at small sizes (often < 3 mm) when locomotion is limited and prey selectivity is dependent on prey distribution (Sanchez-Ramirez 2003). In relatively shallow coastal

and shelf environments, larval fishes may use the entire water column via vertical migration to avoid predation during the day and feed at night (Brewer and Kleppel 1986). Poor habitat quality caused by low oxygen levels in bottom waters may restrict the vertical distribution of organisms present (i.e., behavioral avoidance), possibly leading to higher encounter rates between larval fishes and their prey, and predators (Breitburg et al. 1999), either facilitating, or hindering, the ability of larvae to feed and grow.

Although many studies have looked at the effects of hypoxia on fishery-important species, relatively few have examined ecologically important non-fishery species. For example, forage fish species such as the Atlantic Bumper are extremely abundant in the GoM, often comprising the majority of year-round trawl catch as adults (Hazen et al. 2009, Craig 2012). Atlantic Bumper primarily feed on zooplankton and smaller fishes (Chaves and Umbria 2003), and are in turn fed on by larger piscivores, mammals, and birds (Shaw and Drulliger 1990), functioning as an efficient linkage between lower and higher trophic levels (Hazen et al. 2009, Robinson et al. 2014). Atlantic Bumper spawn in summer months, and while it has been shown that adult Atlantic Bumper avoid hypoxia, less motile early life stages may not be able to do so (Leffler and Shaw 1992).

The overall goal of this work is to examine impacts of hypoxia on larval fishes in the northern GoM. The original objectives of this study were to compare the abundance, diet, growth, condition, and zooplankton prey fields of larval Atlantic Bumper collected in hypoxic and normoxic water masses. However, depth-discrete plankton samples collected within near-bottom hypoxic water yielded too few larval fish specimens for analyses. Therefore, the objectives were revised to address the same comparisons of larval Atlantic Bumper collected from "fully normoxic" and “partially normoxic" water

columns, the latter having an upper normoxic layer and a lower, hypoxic layer. Because the presence of a hypoxic layer influenced the distribution of larval Atlantic Bumper, I hypothesized that the constricted distribution may have negatively impacted larvae with respect to diet, growth, and condition.

3.2 Materials and Methods

3.2.1 Study Region and Water Mass Characterization

Plankton samples and oceanographic data were collected during a research cruise in the northern GoM off the coast of Alabama and Mississippi from July 23-30, 2016 (Figure 3.1). Historically, the region of the stations (n=2) east of Mobile Bay is least

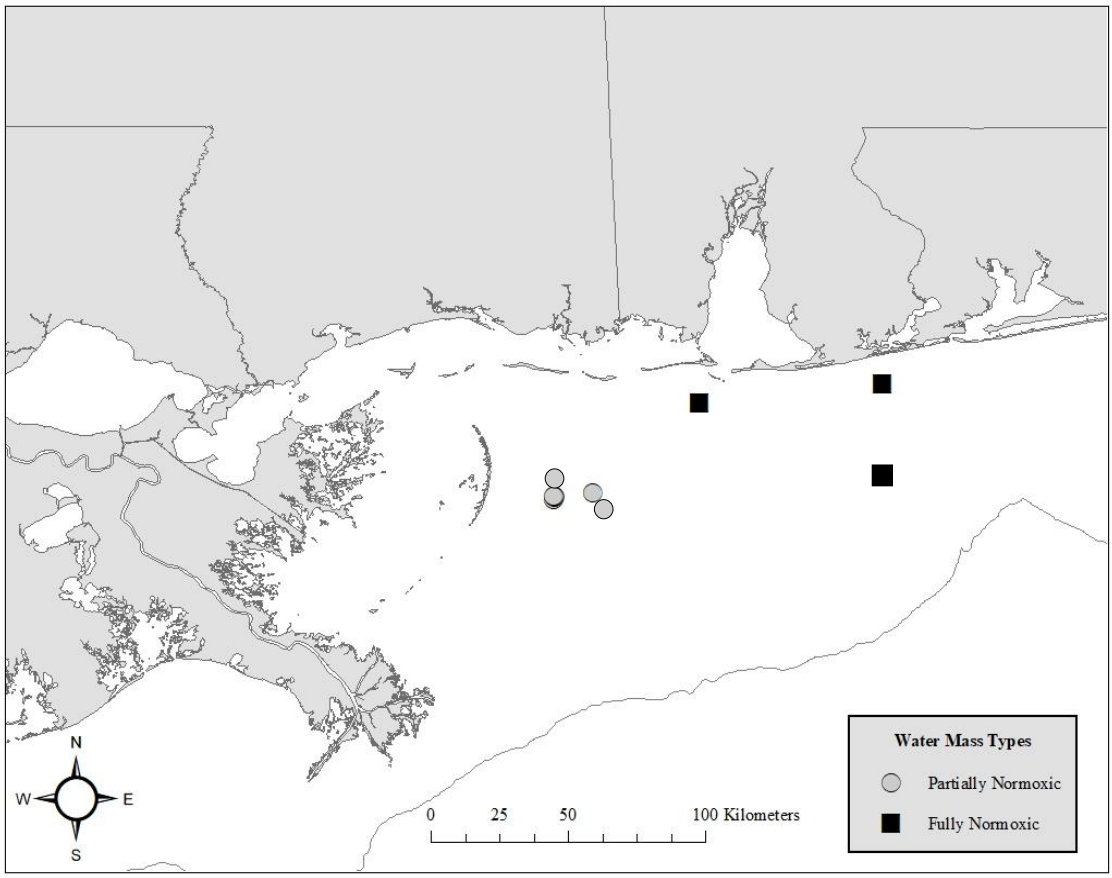

Figure 3.1 . Locations of plankton stations sampled during the 2016 research cruise. Black squares (n=3) indicate stations with a fully normoxic water column. Gray circles (n=7) indicate stations with a partially normoxic water column (bottom hypoxia was present).

impacted by freshwater discharge relative to regions south and west of Mobile Bay, and therefore generally more oligotrophic and less likely to experience bottom hypoxia. The region of the station (n=1) south of Dauphin Island receives freshwater input from Mobile Bay, as well as several barrier island passes. Hypoxic conditions can occur in this region when discharge rates are high and mixing rates of the water column are low enough to allow for stratification (Park et al. 2007). Stations in the Mississippi Bight region near the Chandeleur Islands (n=7) are generally more likely to experience hypoxia due to freshwater input (and nutrient loading) from the Mississippi River, the barrier island passes, Lake Pontchartrain, and smaller river systems (Brunner et al. 2006). Water depths at each station ranged from 17 to 32 m.

Profiles of dissolved oxygen, temperature, and salinity observations were collected at each station using a Seabird Electronics Inc. 911 plus CTD. Plankton sampling stations were categorized as either fully normoxic or partially normoxic based on the dissolved oxygen profiles. Fully normoxic sampling stations were characterized by dissolved oxygen levels > 4 mg/L throughout the entire water column. Partially normoxic sampling stations were characterized by dissolved oxygen levels < 4 mg/L in the lower water column.

3.2.2 Ichthyoplankton and Zooplankton Collection

Depth-discrete plankton samples (n=58) were collected at fully normoxic (n=3) and partially normoxic (n=7) stations using a Bedford Institute of Oceanography Net Environmental Sampling System (BIONESS; 0.25 m2 opening) (Table 3.1). The BIONESS was equipped with a General Oceanics flowmeter to calculate the volume filtered for each sample, and fitted with six 333-µm mesh nets and three 202-µm mesh

nets. The BIONESS was fished in a tow-yo pattern and collected depth-discrete samples at predetermined depth bins (near surface, mid-water, and near-bottom) based on the depth of water column (Table 3.1). Samples were preserved in 95% ethanol, which was replaced after 24 hours, and eventually transferred to 85% ethanol in the lab. Samples were sorted for Atlantic Bumper larvae and zooplankton, which were identified, enumerated, and standardized to the volumes filtered in order to calculate taxon-specific concentrations (number per cubic meter)

Atlantic Bumper larval concentrations were log+1 transformed and compared between regions using a t-test. Total zooplankton concentrations were compared between the water mass types using non-parametric Kruskal-Wallis tests. Because copepods are a common prey item for larval Atlantic Bumper, total copepod (calanoid, cyclopoid, and harpacticoid) concentrations were compared between water masses using a Kruskal-Wallis test. Due to the limited number of Atlantic Bumper larvae collected, samples from hypoxia layers were removed from the analyses, and comparisons of diet, growth, condition, and available larval prey fields were made for Atlantic Bumper collected in fully normoxic water columns to those collected from the normoxic "surface" layer of partially normoxic water columns. Therefore, samples from three stations were dropped altogether, and the following analyses of larval condition, diet, growth, and zooplankton prey fields included eight samples from fully normoxic stations (Station 1 and Station 2), and eight samples from partially normoxic stations (Stations 5,6,8-10).

Table 3.1 Summary of plankton samples collected at fully normoxic and partially normoxic plankton stations off the coast of Alabama and Mississippi during July 2016. Asterisks (*) denote stations that were removed from analyses of larval Atlantic Bumper diet, growth and condition due to low numbers of larval specimens.

Station No.	Tow No.	Date (in 2016)	Depth (m)	Day/ Night	Category	No. Samples (Bin Depth Range)		Larval Conc. no./m^3 (SE)	
						Upper	Lower	Upper	Lower
1	53	July 25	17	Day	Normoxic	n=3 (1-4 m)	n=3 (8-12 m)	7.1 (0.6)	75.6 (6.2)
2	55	July 26	18	Day	Normoxic	n=3 (1-5 m)	n=3 (10-15 m)	0.1 (0.0)	1.9 (0.2)
3*	56	July 26	38	Night	Normoxic	n=3 (1-8 m)	n=3 (14-20 m)	2.6 (1.5)	0.7 (0.5)
4*	57	July 78	23	Night	Partially Normoxic	n=3 (1-7 m)	n=3 (13-20m)	18.5 (8.3)	2.3 (1.4)
5	58	July 28	23	Night	Partially Normoxic	n=3 (1-8 m)	n=3 (14-20 m)	9.3 (2.2)	1.8 (0.7)
6	59	July 28	23	Day	Partially Normoxic	n=3 (1-9 m)	n=3 (15-20 m)	10.8 (6.8)	0.1 (0.0)
7*	60	July 29	32	Night	Partially Normoxic	n=3 (1-10 m)	n=3 (20-30 m)	8.6 (0.6)	1.0 (0.3)
8	61	July 29	31	Night	Partially Normoxic	n=3 (1-10 m)	n=3 (20-30 m)	6.6 (3.3)	0.2 (0.0)
9	62	July 30	23	Night	Partially Normoxic	n=2 (1-8 m)	n=3 (15-22 m)	6.1 (2.9)	0.1 (0.1)
10	63	July 30	22	Day	Partially Normoxic	n=2 (1-8 m)	n=3 (15-22 m)	2.2 (1.3)	0 0

3.2.3 Zooplankton Assemblage Analysis

Group-averaged, Hierarchical Cluster analysis on a Bray-Curtis similarity matrix was used to determine whether zooplankton composition (larval fish prey) varied between fully normoxic and partially normoxic water columns. A similarity profile (SIMPROF) identified homogeneous groups based on zooplankton composition (α = 0.05; 1000 permutations). Significant differences in zooplankton composition between groups determined by SIMPROF were tested with an Analysis of Similarity (ANOSIM). Similarity Percentage (SIMPER) analysis was then used to identify the zooplankton taxa accounting for most differences in assemblage structure between fully partially normoxic water columns.

3.2.4 Larval Atlantic Bumper Morphometric Analysis

A morphometric analysis was conducted on a suite of measurements collected from digital images to provide an estimate of larval Atlantic Bumper condition. Atlantic Bumper larvae were imaged with a Canon EOS Rebel T3i digital camera system mounted onto Zeiss Stemi 2000-C dissecting microscope and then measured to nearest 0.1 mm using iSolutionLite Software. In order to minimize the effect of ontogenetic variability in growth and body shape (Leffler and Shaw 1992, Sanchez-Ramirez 2003), larvae selected for analyses were restricted to a size range of 3-4 mm. The following measurements (to the nearest 0.001 mm) were included in the analyses: notochord length (NL), depth at anus (DA), depth at pectoral fin (DPF), head length (HL), head height (HH), eye diameter (ED), and lower jaw length (LJL). Each measurement was then log-transformed and standardized to create size-independent values using the method described by Lleonart et al. (2002):

$$Y_i^* = Y_i(X_m/X_i)^b$$

Where Y_i* is the size-corrected value of a measurement, Y_i is the observed measurement of an individual "i", X_m is the mean notochord length of all larvae, X_i is the notochord length of the individual larva "i", and b is the within-treatment slope of the log-transformed regression of a morphometric category (e.g., depth at pectoral fin, eye diameter, etc.) and notochord length. Because size corrected measurements correlated with each other, a principal component analysis (PCA) was performed using all the size-corrected measurements in order to obtain independent components of shape, a proxy for body condition, between water mass types. Loading scores of size-corrected variables for a given PC were considered significantly correlated to PC structure when values exceeded 0.4 (or were less than -0.4) (McGarigal et al. 2000). The scores of the first two principal components were then used as a proxy of larval fish condition and compared between water mass types using a Wilcoxon test.

3.2.5 Larval Atlantic Bumper Diet Analysis

Stomach contents from 133 larvae were analyzed following protocols outlined in Llopiz and Cowen (2008) and Carassou et al. (2009) in order to describe and compare larval Atlantic Bumper diets between fully and partially hypoxic water columns. Larvae with missing or empty stomachs were removed from analyses. Alimentary canals were removed under a Leica MZ9.5 dissecting microscope, and gut contents were enumerated and identified into prey categories. Differences in diet composition of larval Atlantic Bumper between fully and partially normoxic water columns were explored by Cluster and Multi-dimensional scaling (MDS) analyses, constructed from a Bray-Curtis similarity matrix in PRIMER.

3.2.6 Larval Atlantic Bumper Growth Analysis

Otolith increment analysis was used to determine recent growth in larval Atlantic Bumper. Sagittal otoliths were removed from each larva and mounted onto glass slides with CrystalBond™ adhesive. Some otoliths required additional preparation and were polished using 3M lapping film (30 or 3.0 µm). Otoliths were then imaged with a Canon EOS Rebel T3i digital camera system mounted onto an Olympus compound microscope using the 1000x oil immersion lens. Radii were drawn along the longest axes of the otoliths to minimize reader error. The left otolith was then aged (unless damaged) independently by two readers. Reader agreement had to be within 10% of one another, or the otolith was read a third time (Sponaugle et al. 2005). If the third read was not within 10% of the first two reads, the otolith was discarded. In cases where age was only one day apart between readers, but greater than 10%, readers discussed the otolith and agreed upon an age. Increments were measured from the outer edge to the outer edge of the subsequent increment Pepin (2001). The outer edge of the otolith, which may not represent a full day's growth, was not included. The last three increments were averaged as a proxy for recent growth, and reader agreement followed the same protocol as aging. A random number generator determined which reader's measurements would be used for analysis. Differences in recent growth of larval Atlantic Bumper between the two water column types were tested by a Wilcoxon test.

3.3 Results

3.3.1 Study Region and Water Column Characterization

Originally, 10 stations were sampled in the Mississippi Bight, with fully normoxic stations (Figure 3.2 a, b, c), located east and south of Mobile Bay (Figure 3.1), and 7

partially normoxic stations east of the Chandeleur Islands (Figure 3.2 d-j). However, due to a lack of larvae at several of the stations, one fully normoxic, (Station 3) and two partially normoxic stations (Stations 4 and 7) were removed from analyses (Table 3.1). In general, fully normoxic stations that remained in the analyses were shallower (17m to 18m) than the partially normoxic stations (22m to 31m) (Table 3.1, Figure 3.2).

3.3.2 Ichthyoplankton and Zooplankton Collection

Larval Atlantic Bumper abundance was highly variable across the sampling stations. In general, Atlantic Bumper larvae were found in near-bottom waters in a fully normoxic water column, and in the upper portion of a partially normoxic water column (Figure 3.3). There was a marginal difference in larval abundance between the fully and partially normoxic stations (t-test, $t = 1.97$; $p = 0.06$) (Figure 3.4). Due to the limited number of Atlantic Bumper larvae collected, samples from hypoxic layers were removed, and comparisons of diet, growth, condition, and available larval prey fields were made for Atlantic Bumper collected in fully normoxic water columns to those collected from the normoxic "surface" layer of partially normoxic water columns. Therefore, samples from three stations were dropped altogether, and the following analyses of larval condition, diet, growth, and zooplankton prey fields included eight samples from fully normoxic stations (Stations 1 and 2), and eight samples from partially normoxic stations (Stations 5,6,8-10). Zooplankton abundance (Wilcoxon test, $Z = 0.38$, $df = 1$, $p = 0.54$) (Figure 3.5) and total copepod abundance (Wilcoxon test, $H = 0.001$, $df = 1$, $p = 0.97$) (Figure 3.5) did not differ between the fully and partially normoxic water masses. Calanoid and cyclopoid copepods, chaetognaths, siphonophores, and doliolids were among the dominant zooplankton (in at least 50% of the samples).

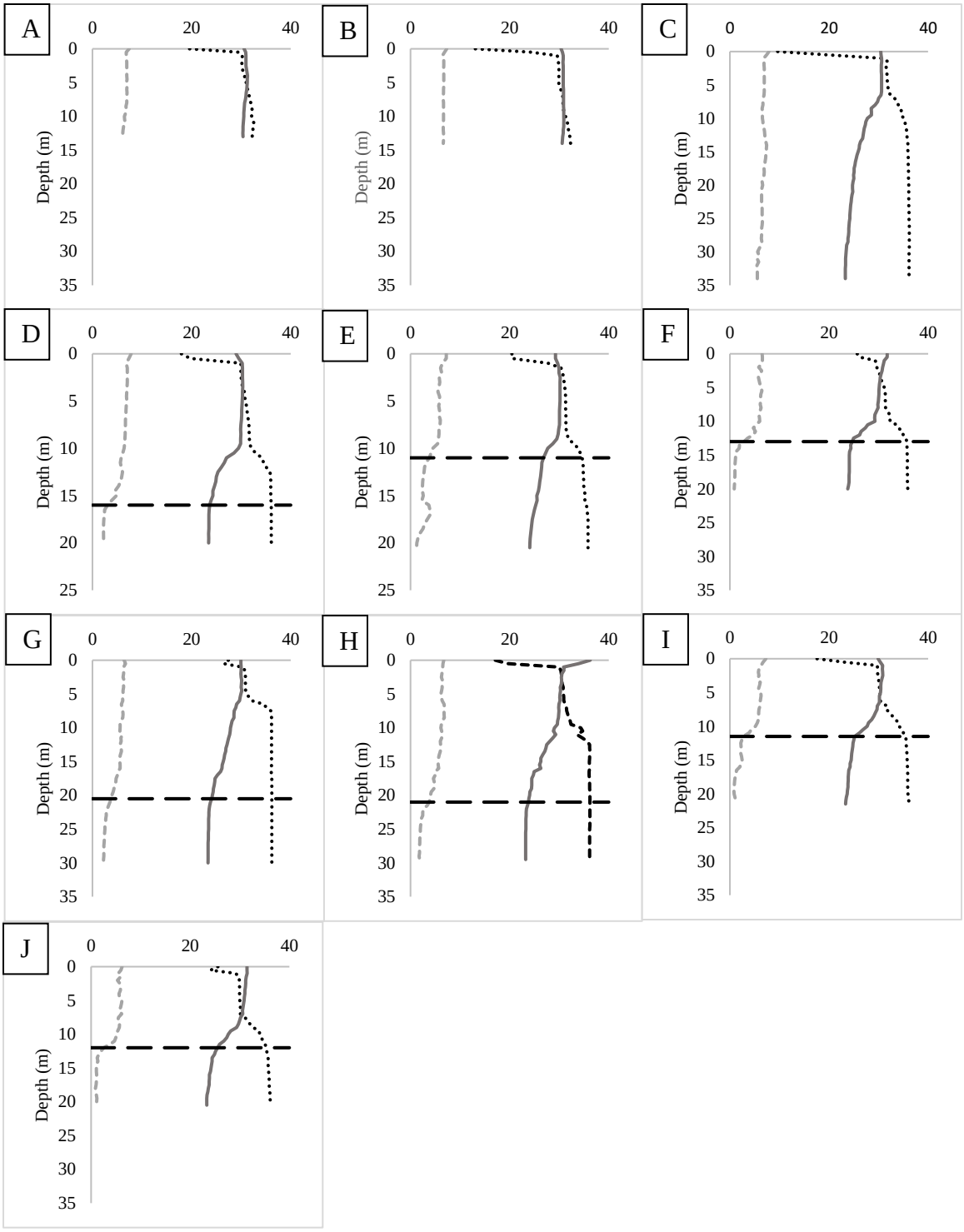

Figure 3.2 Depth profiles of salinity (dotted), temperature (solid, ℃) and dissolved oxygen (vertical short dashed, mg/l) at sampling stations with a fully normoxic water column (A-C) and a partially normoxic water column (D-J). The horizontal, long dashed line denotes the depth at which hypoxia (DO < 4 mg/l) was observed.

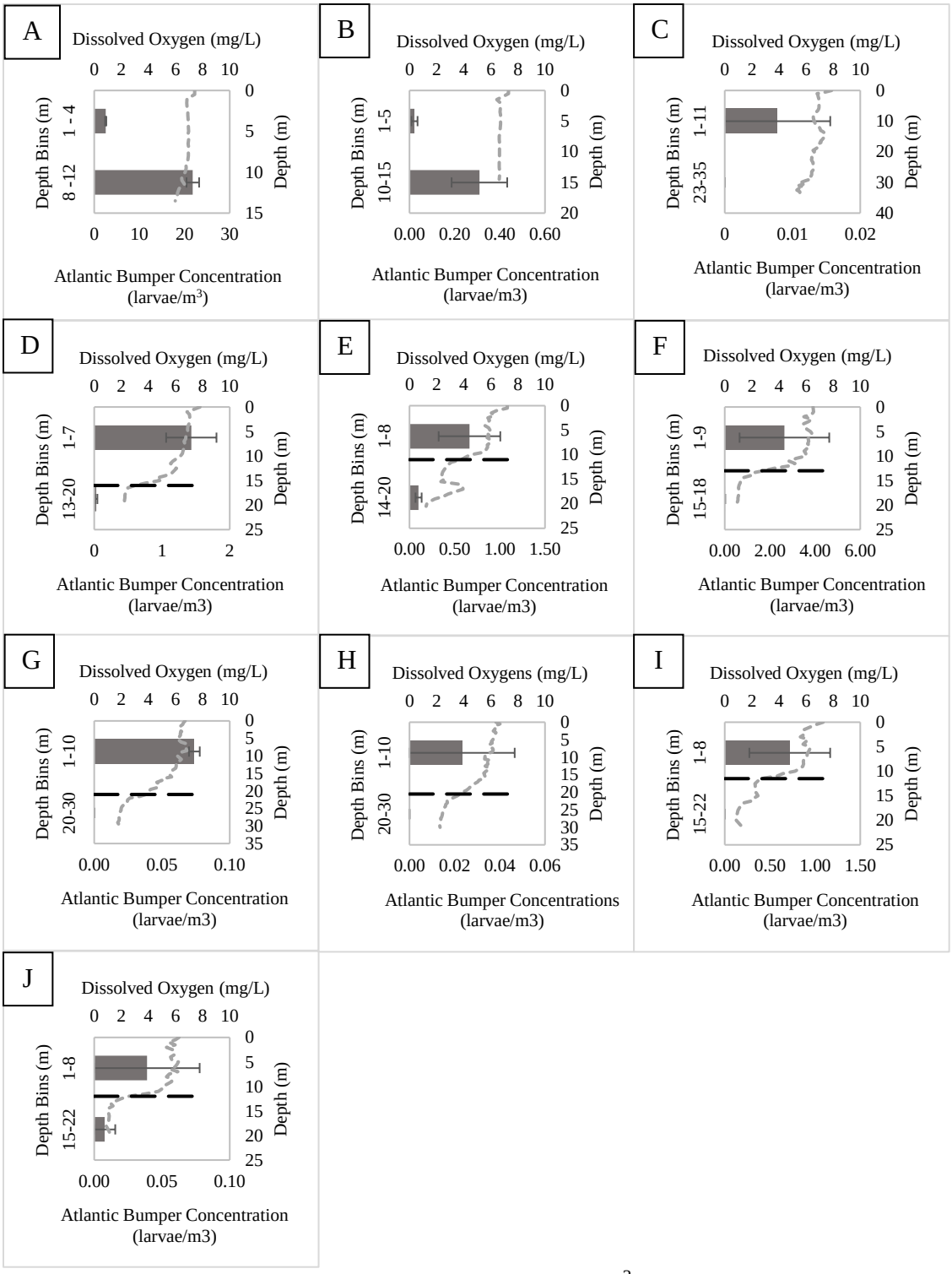

Figure 3.3 Larval Atlantic Bumper abundances (larvae/m^3) within sampled depth bins of the 10 stations sampled in fully normoxic (A-C) and partially normoxic (D-J) water columns. The small-dashed line represents the dissolved oxygen (mg/L) profile for the water column in which the samples were taken. The horizontal, long-dashed line represents the depth at which hypoxia (<4mg/L) was observed.

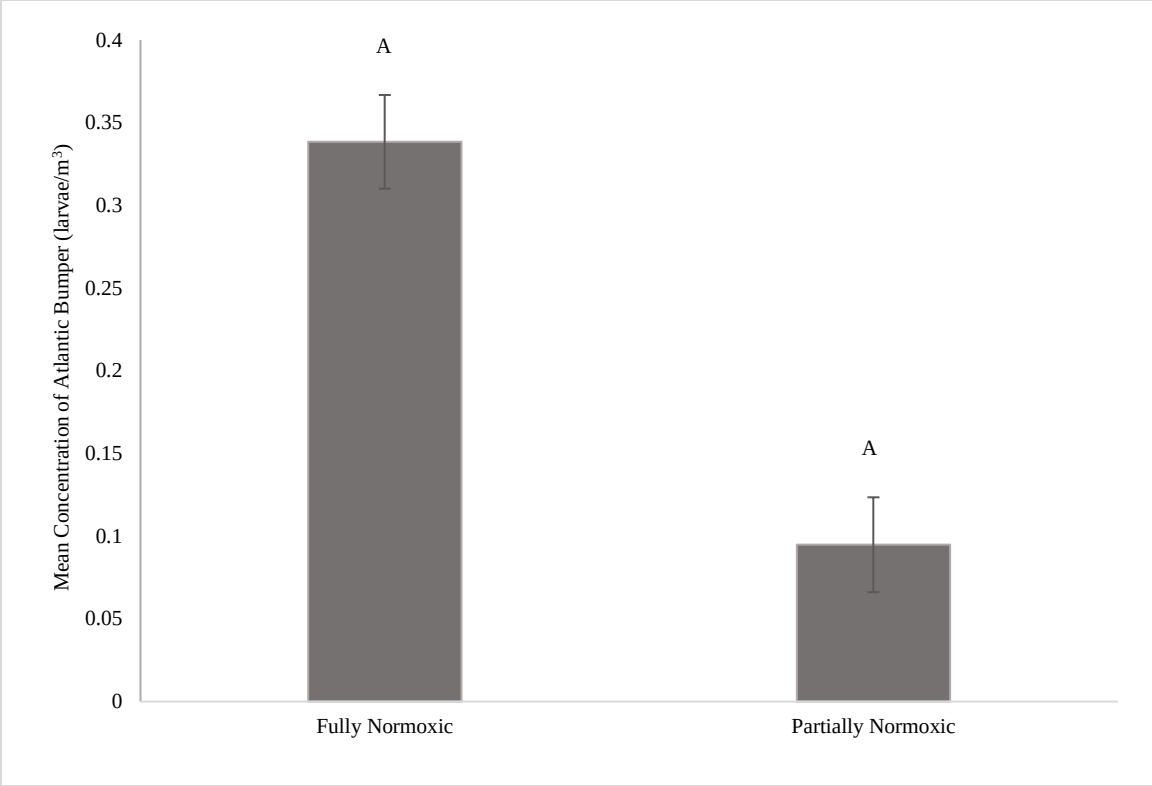

Figure 3.4 Mean concentration (larvae/ m^3) of Atlantic Bumper larvae from samples collected within fully normoxic (n = 18) and partially normoxic (n = 40) water masses. Concentration values have been log+1 transformed. Error bars represent standard error. Letters indicate significance among water masses based on a t-test.

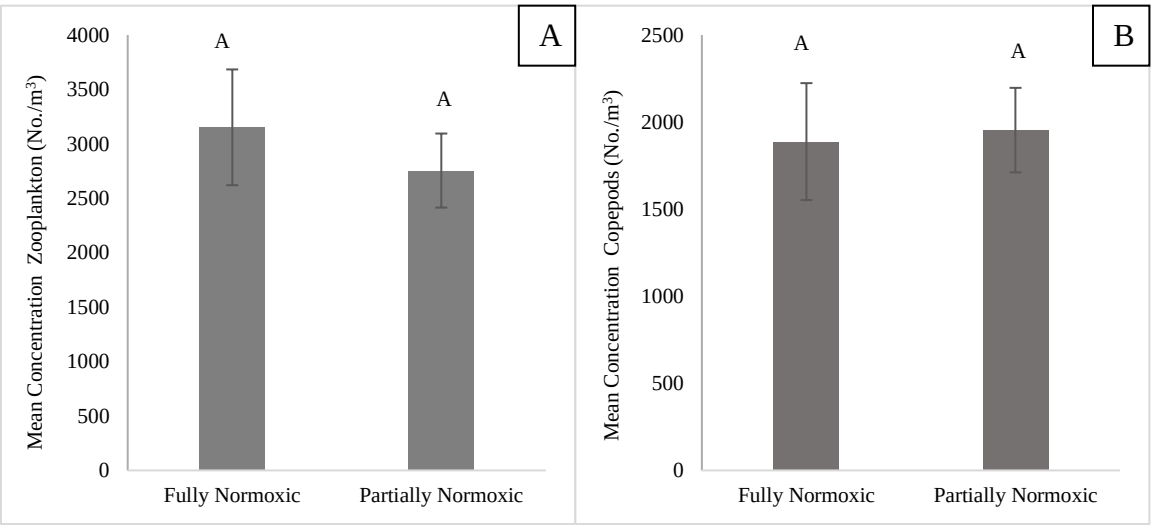

Figure 3.5 A) Mean concentration of zooplankton (No./ m^3) from samples collected within fully normoxic (n = 18) and partially normoxic (n = 38) water masses. B) Mean concentration of total copepods (No/m^3) from samples collected within fully normoxic (n = 18) and partially normoxic (n = 38) water masses. Error bars represent standard error. Letters indicate significance among water masses based on a Kruskal-Wallis test.

3.3.3 Zooplankton Assemblage

Cluster analysis revealed two homogenous groupings using SIMPROF. ANOSIM revealed that each cluster was significantly different from each other ($R^2 = 0.507$, $p = 0.01$) (Figure 3.6). The first cluster included four partially normoxic samples. The second cluster was a mixture of both fully and partially normoxic samples. A SIMPER analysis revealed that cladocerans, ascidians, bivalve larvae, larvaceans, doliods, crab zoea, calanoid copepods, cyclopoid copepods, and hydromedusae contributed to 52% of the dissimilarity among the water mass types (Table 3.2).

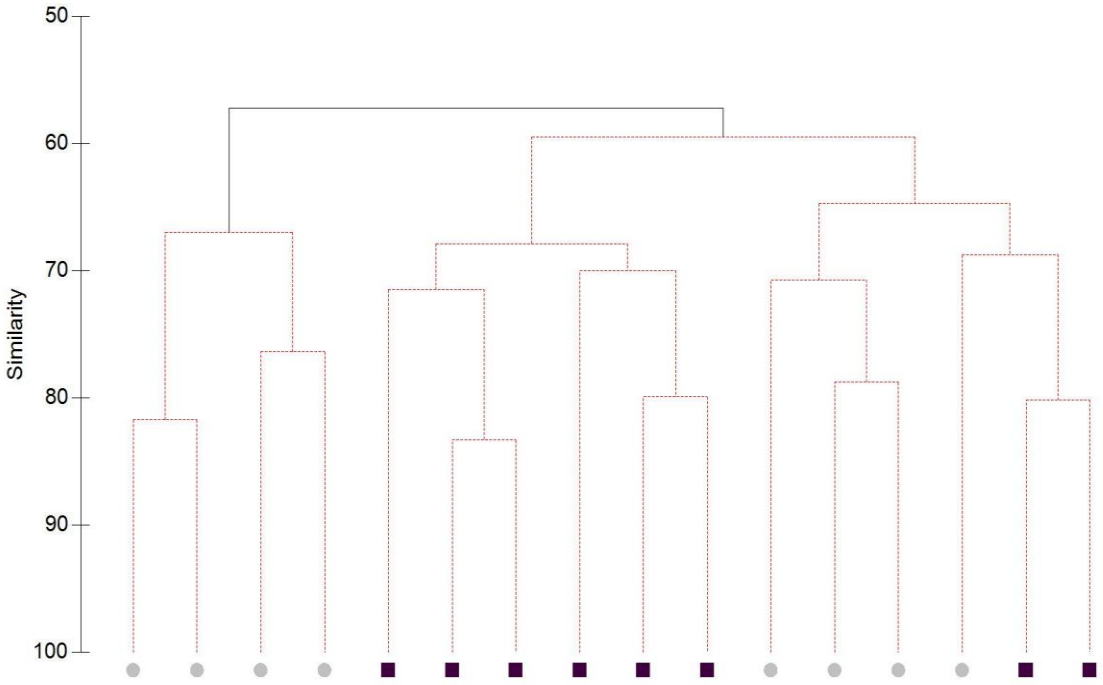

Figure 3.6 Results of a Cluster analysis of zooplankton collected within fully normoxic (squares) and partially normoxic (circles) water mass types. Two clusters are shown via the dotted brackets, which indicate homogeneity.

Table 3.2 Results from a SIMPER analysis of zooplankton abundances between fully normoxic and partially normoxic water columns. Av. Abund FN = Average Abundance from Fully Normoxic samples; Av. Abund PN = Average Abundance from samples Partially Normoxic; Av. Diss. = Average Dissimilarity; % Cum. = Cumulative Percentage of Dissimilarity

Species	Av. Abund. FN	Av. Abund. PN	Av. Diss.	% Cum.
Fully Normoxic & Partially Normoxic Average Dissimilarity: 41.07%				
Cladoceran (No./m^3)	194.21	20.9	3.49	8.49
Ascidian (No./m3)	85.29	10.81	2.89	15.54
Doliolid (No./m3)	238.05	36.62	2.51	21.65
Larvacean (No./m3)	58.06	80.62	2.49	27.73
Bivalve larvae (No./m3)	120.31	0	2.46	33.7
Calanoid copepod (No./m3)	2287.58	1912.18	2.2	39.05
Crab zoea (No./m3)	30.19	98.32	2.17	44.34
Cyclopoid copepod (No./m3)	170.63	189.6	1.77	48.65
Hydromedusae (No./m3)	14.81	0.27	1.76	52.93

3.3.4 Larval Atlantic Bumper Morphometrics

In total, 125 larval Atlantic Bumper were used for morphometric analysis (fully normoxic: n=87, partially normoxic: n=38). Of the 6 PCs extracted from the PCA, the first two explained 65.5% and 15.2% of the variation respectively (80.7% total) (Table 3.3). DPF, DA, and HL loadings were significantly negatively correlated to PC1, while HL and DPF were significant in PC2, with HL being positively correlated and DPF being negatively correlated. A negative loading indicates an inverse relationship of the associated variable to the values of the PC. Hence, as PC1 increases, the relative values of DPF, DA, and HL decrease. Both PC1 scores (Wilcoxon test, $Z = 4.24$, $df = 1$, $p = 0.040$) and PC2 scores (Wilcoxon test, $Z = 14.28$, $df = 1$, $p < 0.001$) were significantly different between the two water masses (Figure 3.7), with mean scores of the partially

normoxic samples being smaller. Because of the inverse relationship indicated by the negative loading scores, this means that the DPF, DA, and HH were relatively greater in larvae collected in a partially normoxic water column.

Table 3.3 Results from a PCA of the measurements taken on larval Atlantic Bumper in both fully normoxic samples and samples above hypoxia. Values above 0.4 (-0.4) are considered significant (McGarigal et al. 2000).

Variable	PC1	PC2
Depth at Pectoral Fin (DPF)	-0.575	-0.478
Depth at Anal Fin (DA)	-0.569	-0.09
Head Length (HL)	-0.288	0.839
Head Height (HH)	-0.491	0.108
Eye Diameter (ED)	-0.074	0.136
Lower Jaw Length (LJL)	-0.126	0.169
Variance explained (%)	65.5	15.2

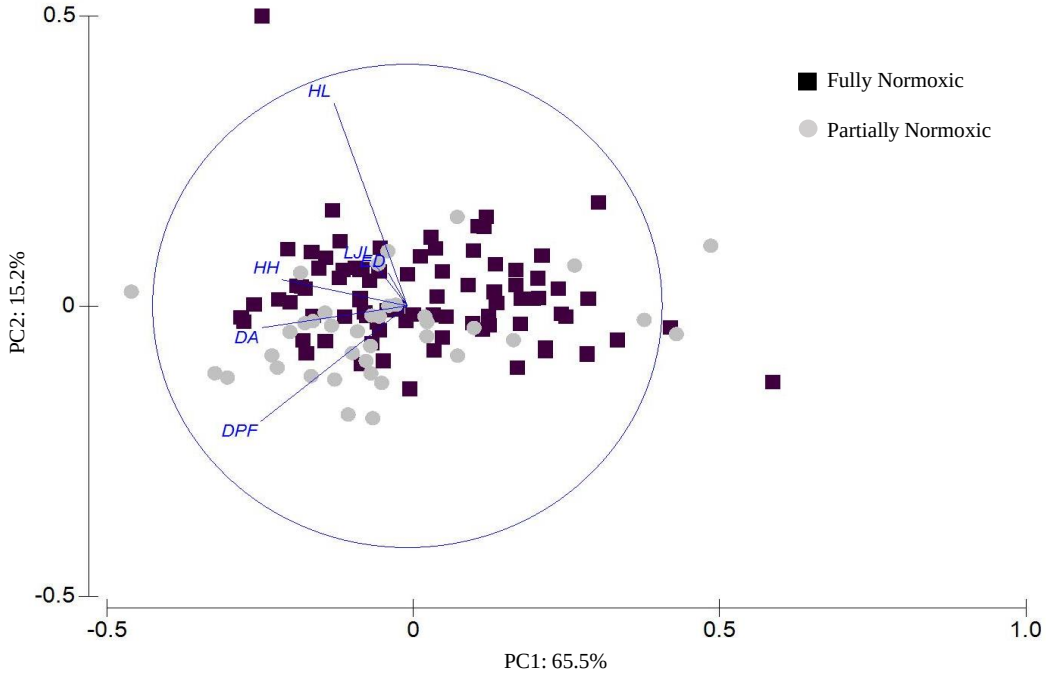

Figure 3.7 Results from a Principal Component Analysis of the measurements taken on larval Atlantic Bumper. Each circle represents an individual larva. Larvae collected in a fully normoxic water column are represented by squares. Larvae collected above hypoxia are represented by circles.

3.3.5 Larval Atlantic Bumper Diet

Approximately 90% of the Atlantic Bumper larvae collected in the fully normoxic water column contained identifiable gut contents, while only 10% of the larvae from the partially normoxic water column contained identifiable gut contents. In total, the stomach contents of 121 Atlantic Bumper larvae were analyzed for diet composition (fully normoxic: n=80; partially normoxic: n=41). The average number of prey per larva was significantly different as revealed by a Wilcoxon test ($Z = 57.10$, $df = 1$, $p < 0.001$) (Figure 3.8). Cylopoid copepods were the most common prey item in larvae from fully normoxic samples with (%FO=of 23%), and all copepod categories combined comprised over 44% of their stomach contents (Table 3.4, Figure 3.9). Copepod pieces (31.25%) were most common in larvae collected in a partially normoxic water column (Table 3.4). The diet compositions of 77 larval Atlantic Bumper with identifiable gut contents were available for the MDS analysis, however the sample size from the fully normoxic water column (n=71) was much greater than that of the partially normoxic water column (n=6). The MDS analysis revealed that the diet did not differ among the fully normoxic and partially normoxic water columns (Figure 3.10).

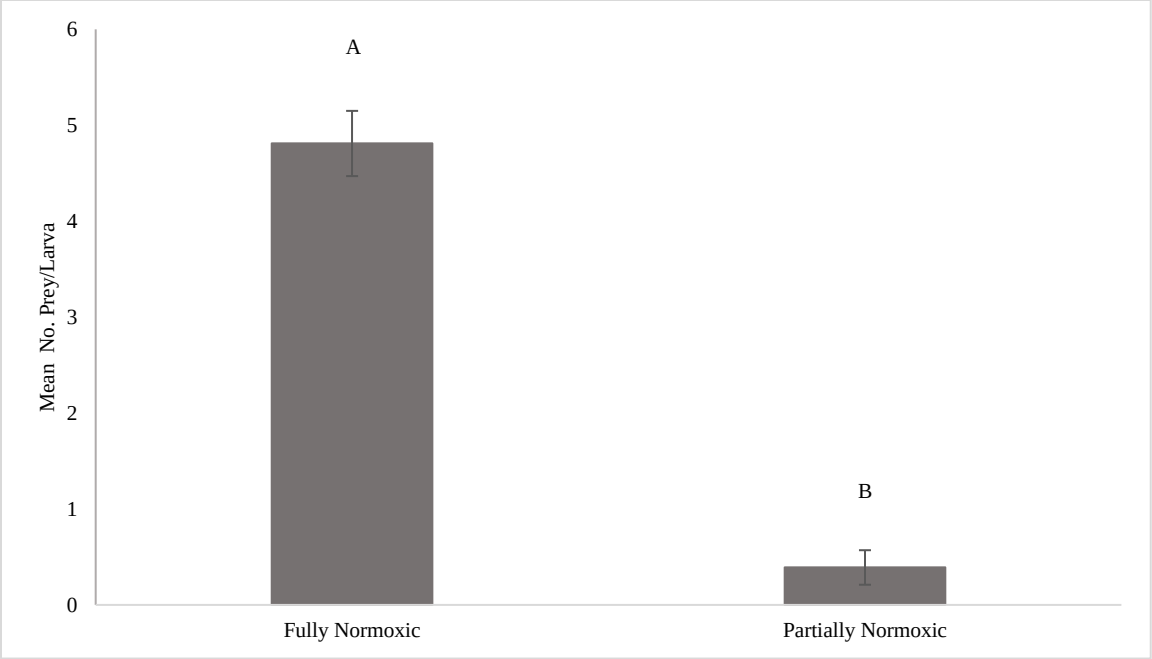

Figure 3.8 Mean number of prey items found per larval between the two water mass types. Error bars represent standard error. Letters indicate significant differences between water mass types based on a Wilcoxon test.

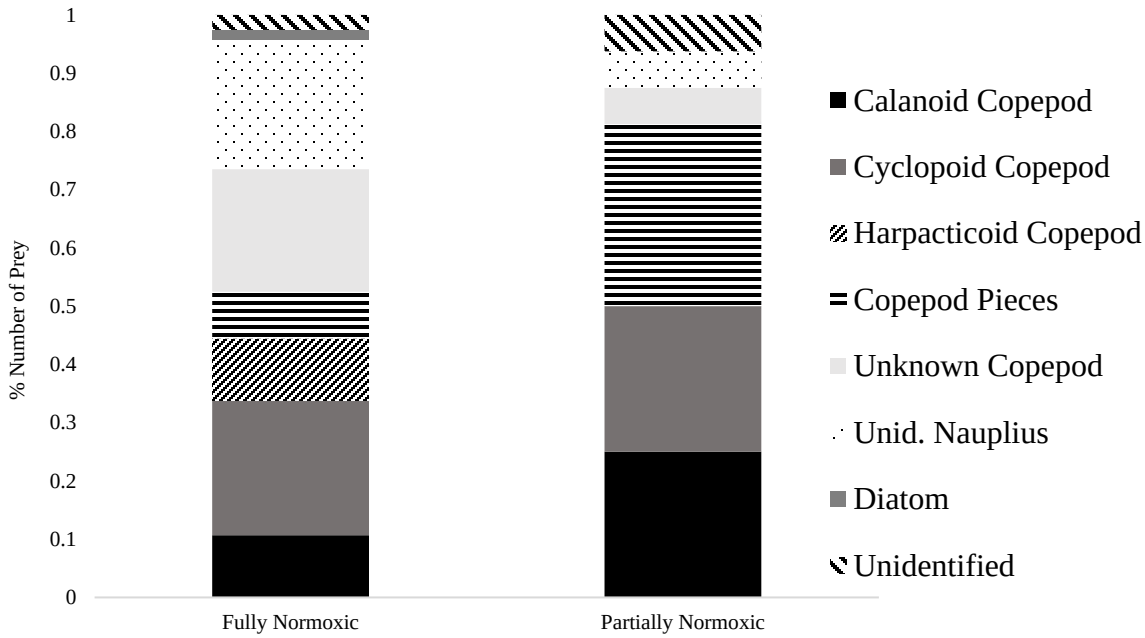

Figure 3.9 Percentages of identified prey in the guts of Gulf Menhaden larvae from the three water masses.

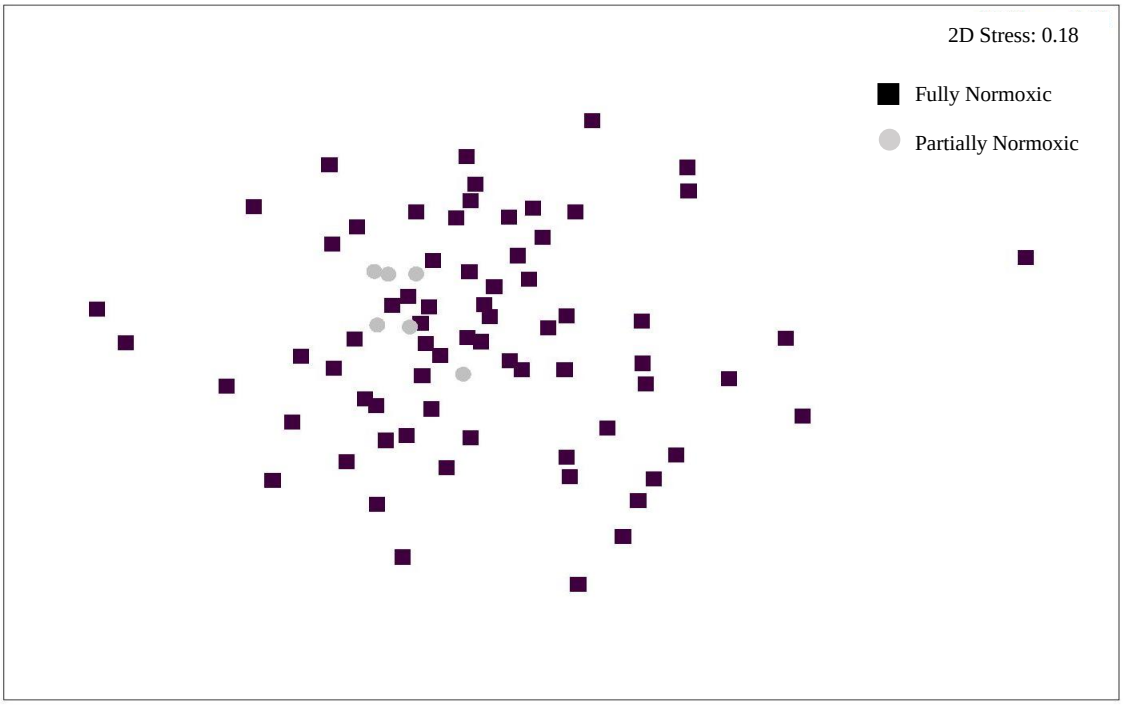

Figure 3.10 Results from a multi-dimensional scaling analysis of the diets of larval Atlantic Bumper from fully normoxic (squares) and partially normoxic (circles) water columns. Each circle represents an individual larva.

Table 3.4 Gut content analysis of 121 Atlantic Bumper larvae. %N = percent of the total prey items (N) found in that water column type: FO = frequency of occurrence; %FO = percent frequency of occurrence among larvae containing food; n = the total number in each category.

	Water Masses							
	Fully Normoxic				Partially Normoxic			
Prey Item	n	%N	FO	%FO	n	%N	FO	%FO
Calanoid Copepod	41	10.65	28	35	4	25	3	7.32
Cyclopoid Copepod	89	23.12	44	55	4	25	3	7.32
Harpacticoid Copepod	41	10.65	24	30	-	-	-	-
Copepod Pieces	31	8.05	18	22.5	5	31.25	3	7.32
Unknown Copepod	81	21.04	43	53.75	1	6.25	1	2.44
Unid. Nauplius	86	22.34	44	55	1	6.25	1	2.44
Diatom	6	1.56	6	7.5	-	-	-	-
Unidentified	10	2.60	7	8.75	1	6.25	1	2.44
Total Prey	385				16			
Num. of Fish	80				41			
Num. of Empty Guts	8				35			

3.3.6 Larval Atlantic Bumper Growth

Recent growth was examined using otolith increment analysis for a total of 78 larval Atlantic Bumper (fully normoxic: n=50; partially normoxic: n=28). No significant difference in recent growth was observed in larvae collected between the fully normoxic and partially normoxic water columns (Wilcoxon test, Z = 0.012, df = 1, p = 0.9129) (Figure 3.11).

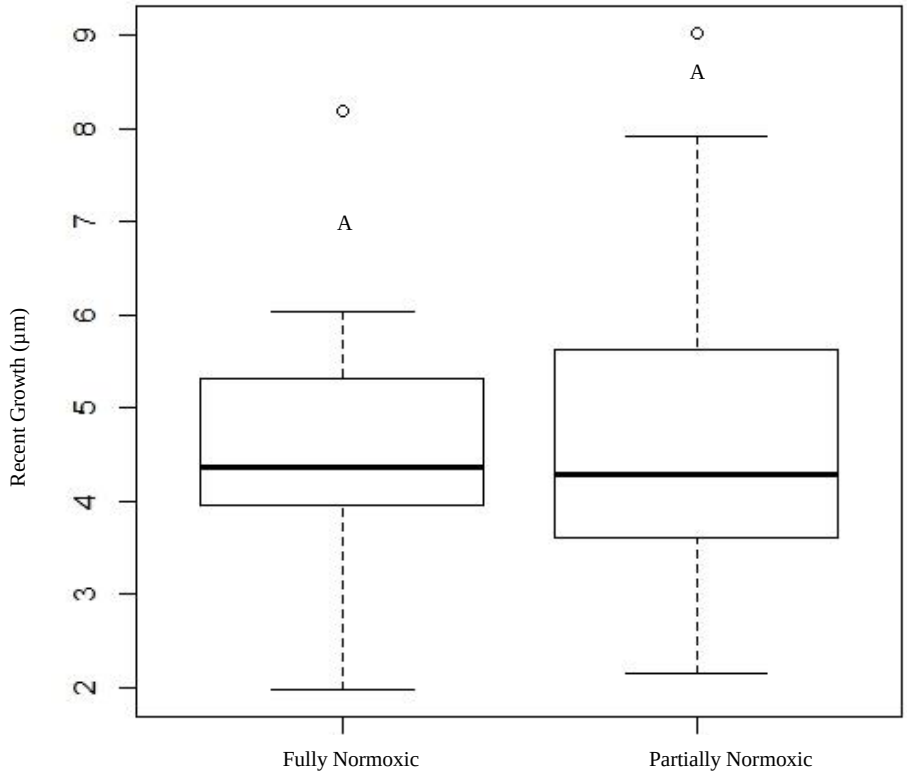

Figure 3.11 Comparisons of recent growth of larval Atlantic Bumper. The bold line within each box represents the median of the distribution of recent growth for each water mass, and the upper and lower portion of each box represent the first and third quartiles. The ends of the "whiskers" (dashed lines) represent the minimum and maximum values. Open circles outside of the whiskers are outliers. Letters indicate significant differences among water masses based on a Kruskal-Wallis test.

3.4 Discussion

The effects of hypoxia in marine ecosystems are often species-specific and stage-dependent, and less motile organisms (like larval fishes) are often the most susceptible. Previous studies have mostly targeted demersal, fisheries-important species; however, highly abundant forage fishes, such as Atlantic Bumper, play a key role in trophic systems, feeding on many lower trophic level organisms, and in turn being predated on by many high trophic level species, and should be included when considering ecosystem effects of environmental perturbations such as hypoxia. It has been hypothesized that behavioral avoidance of bottom-hypoxia can lead to the aggregation of plankton in the normoxic layer of the water column, with the possibility of impacting larval fish survival positively, or negatively, due to an increase in available prey, or an increase in predators (Breitburg et al. 1999).

In my study, hypoxic regions were generally devoid of Atlantic Bumper larvae, which suggests behavioral avoidance or increased mortality due to predation (Figure 3.3). However, the concentration of larval Atlantic Bumper, as well as zooplankton, did not differ between fully normoxic water column stations and the normoxic, "surface" portion when bottom-hypoxia was present. Total copepod abundance, a proxy for prey availability, was also not significantly different between the two water types, although larvae in the fully normoxic water mass had significantly more prey items in their guts and significantly fewer empty guts. Atlantic Bumper growth (based on otolith increment analysis), an important characteristic related to survival, did not differ between larvae collected in the fully normoxic water and those collected in restricted normoxic water. In contrast, the condition of Atlantic Bumper larvae (as estimate from morphometric

analyses) was significantly higher in the partially normoxic water relative to the fully hypoxic water. Overall, evidence to support the hypothesis that larval Atlantic Bumper larvae restricted to upper, normoxic waters above hypoxia were negatively impacted relative to larvae collected in fully normoxic water columns was equivocal, and the disparity in the growth and morphometric results may reflect variable responses in these two indicators of condition (Table 3.5).

Table 3.5 Summary of biotic and abiotic parameters used in this study to examine patterns of growth and condition in larval Atlantic Bumper collected at sampling stations within three different water masses.

	Stastical Relationship		
Larval Factors			
Growth	Normoxic	=	Hypoxic
Morphometric Analyses	Normoxic	<	Hypoxic
Explanitory Variables			
Copepod Abundance	Normoxic	=	Hypoxic
No. Prey per Larva	Normoxic	>	Hypoxic
% Empty Guts	Normoxic	<	Hypoxic

The physical environments of the fully normoxic and the surface of the partially normoxic stations were also similar. While water temperature at the fully normoxic stations was significantly higher than that observed at the partially normoxic stations, the mean difference was slight (27.8°C vs 25.77°C), and within the expected thermal range (22.7-33 °C) for larval Atlantic Bumper (Ditty et al. 2004). Leffler and Shaw (1992) reported faster growth rates for Atlantic Bumper larvae collected in water temperatures ranging from 29-31°C relative to larvae found at 26.5-29 °C; however, the difference in

temperature among water mass types was not as great in this study. Salinity, another factor that can influence larval fish distribution, also did not differ significantly between fully normoxic and partially normoxic stations. Both temperature and salinity heavily influence community composition, abundance, diet and growth of marine organisms (Tandler et al. 1995, Otterlei et al. 1999, Green and Fisher 2004, Barletta et al. 2005). Similar physical environments between the fully normoxic stations and the partially normoxic stations also supports the finding that growth of the larval Atlantic Bumper was not different between the water mass types, as temperature (in particular) heavily affects larval fish growth (Houde 1989).

The two measures of larval fitness (recent growth and condition) yielded mixed results; recent growth among larval Atlantic Bumper did not differ between the fully normoxic and partially normoxic stations, but larval condition was significantly lower at the fully normoxic stations compared to the partially normoxic stations. These contrasting results are likely due to the sensitivity of each method, and the variability in the time it takes for each measured parameter to reflect the conditional state of the larva at time of collection. Different measures of growth (e.g., morphometrics, RNA/DNA, otolith increments) operate on various time scales. RNA indices have been shown to correlate with growth and can begin to express differentially due to stressors (e.g., starvation) after a day or two (Caldarone and Buckley 1991). Peripheral otolith increment analysis has been shown to indicate starvation events (smaller growth increments) within 1 to 3 days (Govoni et al. 1985); however, relating these results to somatic growth can take up to two weeks (Milicich and Choat 1992). It is unknown how long the hypoxia was present, and the larval Atlantic Bumper in this study may not have been aggregated above hypoxia for

long enough to express any impacts. While growth did not differ, dissimilarities in morphometry were present, with larvae collected above hypoxia being conditioned in terms of having deeper bodies compared to those from a fully normoxic water column. However, morphometric analyses are not sensitive to short term events (Ferron and Leggett 1994), therefore if the hypoxia occurred recently enough (or the larvae were not within the vicinity of the hypoxia long enough) that differences in more-sensitive otolith increment analysis were not expressed, the morphometric dissimilarities observed in this study may not be due to the hypoxia, but may reflect factors such as maternal effects, or environmental conditions (e.g., temperature, prey field) the larvae were exposed to before this study.

I used zooplankton abundance in the fully normoxic and partially normoxic plankton samples as a proxy for the prey field available to larval Atlantic Bumper in each water mass type. Previous studies have reported constricted distributions of both larval fishes and their zooplankton prey when hypoxia is present, forcing larval fishes and zooplankton to aggregate more densely in the normoxic portion of the water column, and leading to higher predator-prey overlap (Greer et al. 2016, Glaspie et al. 2018). Concentration of copepods, an important prey item of larval Atlantic Bumper (Sanchez-Ramirez 2003; this study), was not significantly different between the fully normoxic and partially normoxic water columns. Larval Atlantic Bumper begin exogenously feeding at relatively small sizes (< 3 mm); these preflexion stages have limited mobility, therefore high available prey abundance may be an important factor for successful feeding (Werner and Blaxter 1980, Sanchez-Ramirez 2003). For example, Comyns (1997) found a positive, significant relationship between the number of copepods and larval Atlantic

Bumper growth; however, this relationship became asymptotic at a concentration of copepods far smaller than the concentration observed in this study, suggesting that the amount of copepods available to the larvae was more than sufficient for satiation and would not be a limiting factor.

Although the concentration of prey did not differ between the fully normoxic and partially normoxic stations, the number of prey per larva did, with larvae collected in a fully normoxic water column containing more prey per larva on average than the larvae from a partially normoxic water column. Zooplankton community composition and diet composition of the larvae were not different between the fully normoxic and partially normoxic stations, excluding available prey type as a factor determining the number of prey items consumed. The aggregation of plankton in the normoxic layer of a water column with bottom-hypoxia can have profound effects on the ability of larvae to feed and avoid predators. If predation pressure is increased on the aggregated larval fish, the likelihood of the larvae to capture prey can be reduced, as was seen in Skajaa (2003), which found that when predators were present, larval cod feeding was significantly repressed. Even though the type and amount of prey available to the larval Atlantic Bumper was the same between the fully normoxic and partially normoxic stations, predator avoidance behavior may account for the differences seen in the amount of prey being consumed. While information on predatory organisms was outside of the scope of this study, data on potential predators (e.g., jellyfish, piscivorous larval fishes) may be available through CONCORDE's *I*n *S*itu *I*chthyoplankton *I*maging *S*ystem (ISIIS), which enumerated and identified plankton using line-scan camera imagery (Greer et al. 2018). The ISIIS was fished in a similar fashion to the BIONESS on the research cruise during

which the larval Atlantic Bumper were collected, thereby providing information on relative abundances of predators present in the water column with the larvae, which could possibly correlate to the diet results observed (e.g., number of prey in guts).

In order to avoid predation, as well as feed on migrating zooplankton prey, larval fishes often migrate vertically on a diel cycle (Brewer and Kleppel 1986). Because a large portion of the larval Atlantic Bumper collected in a fully normoxic water column (all samples collected during the day) were at depth, and contained prey, possibly suggesting that Atlantic Bumper larvae prefer to feed during the day in the deeper portion of the water column. This was also observed in a study by Sanchez-Ramirez (2003), which found almost 80% of larval Atlantic Bumper collected during the day (06:40 to 17:40) contained food, while only 13% of larvae collected at night (20:36 to 05:58) contained prey in their guts.

The 10 stations originally chosen were sampled during both day and night, with two stations sampled during the day, and one station sampled at night from a fully normoxic water column, as well as two stations sampled during the day, and five stations sampled at night from the partially normoxic water columns. From the fully normoxic stations it is clear that larval Atlantic Bumper remain at depth during the day, and migrate to the surface at night (Figure 3.3). When hypoxia is present, however, the larvae are found mostly at the surface regardless of time of day (Figure 3.3), suggesting larval Atlantic Bumper avoid hypoxia as the adults have been shown to do (Hazen et al. 2009).

The vertical extent of the hypoxia in this study ranged from 50-74% of the water column; however, the fully normoxic stations were mostly shallower than the partially normoxic stations, indicating that although hypoxia was present, the larvae and

zooplankton still had approximately the same amount of normoxic vertical space for migration. This may explain the similar larval (zooplankton) abundances observed between the fully normoxic and partially normoxic stations. Unfortunately, the sampling design in this study did not allow for a rigorous examination of the possible confounding effects of diel vertical migration; future studies should include these potential interactive effects.

The results seen in this study highlight the difficulty of predicting the effects perturbations such as hypoxia can have on larval fishes, in part because this study was not able to encompass all of the potential factors associated with hypoxia. Parameters important to larval fish survival are influenced by a multitude of factors (physical environment, prey field) and processes (predation, vertical migration), which co-occur, and should be included in analyses to most accurately describe the results observed. This study provided data on environmental factors in relation to parameters important to early life stage survival, which can be used to inform future stock assessment models, as survival to adult stages is an important factor determining subsequent adult stock size (Houde 2002). Additionally, this study provided information on a non-fisheries species, Atlantic Bumper, which are extremely abundant members of coastal ecosystems, and provide important trophic linkages. Stock assessment models of fishes in the GoM often focus solely on fisheries-important species, and do not include environmental variables, inter-species interactions, or stage-specific information, resulting in large variability between what is predicted and what is observed. In order to provide more accurate predictions, future models should include data such as those resulting from this study, that is, stage-specific information on growth and condition in relation to environmental

parameters, as well as information on non-fisheries important forage fish species. Furthermore, as with Chapter I, these data can be used to inform the 4D synthesis model of CONCORDE in terms of plankton layering, and larval Atlantic Bumper growth rates in relation to environmental parameters, which can then be applied to coastal management assessments.

CHAPTER IV – CONCLUSIONS

In this study, I examined the impacts related of two very different freshwater discharge related events on the diet, growth and condition of larval fishes in the northern GoM. In Chapter II, my analyses suggest that the opening of the Bonnet Carre Spillway and increased freshwater discharge from other sources (e.g., Mobile Bay) created highly variable physical conditions within a relatively small region (Mississippi Bight), which resulted in variable diet, growth and condition among larval Gulf Menhaden. In this case, Gulf Menhaden larvae in the lower salinity, higher turbidity stations (Chandeleur Sound) were most negatively impacted. In Chapter III, I observed relatively little variation in physical & biological properties among stations sampled in the same general region, with the exception of bottom hypoxia. Larval Atlantic Bumper diet and growth did not differ between fully and partially normoxic water columns, and few negative impacts were detected with respect to the restriction of larval Atlantic Bumper vertical distribution. Combined, my results suggest that while the environmental impacts related to riverine discharge may be predictable, larval fish responses to such events are highly variable. This discrepancy in results shows how the impacts of riverine discharge are difficult to predict, and highlights the need for large scale efforts in which as many environmental factors as possible can be included.

An overarching goal of the CONCORDE project is to develop a 4D-synthesis model to describe relevant physical-biological processes and the resulting distributions of organisms in a nearshore river-dominated ecosystem (Greer et al. 2018). Contributions to the model include information on zooplankton and ichthyoplankton vertical distributions, as well as larval fish growth rates, with respect to variable physical conditions (e.g.,

stratification hypoxia, temperature and salinity gradients, etc.). Therefore, the observations of larval Gulf Menhaden and Atlantic Bumper distributions and vital rates described in my study directly contribute to the goals of CONCORDE, and will provide valuable data to inform the model, the results of which can be applied to management of coastal systems, assessments of risk, and examination of how ecosystem-level impacts of oil may vary with season (Greer et al. 2018).

Furthermore, the type of research conducted here may have future applications related to fisheries and ecosystem management (NMFS 2016). Currently, very few stock assessment models include environmental factors, with the notable exception of the inclusion of harmful algal bloom information in the assessments of Red Grouper and Gag Grouper (SEDAR 33 2014, SEDAR 42 2015). In an attempt to improve population assessments and move away from single-stock analyses, NOAA is moving toward Ecosystem Based Fisheries Management (EBFM) initiatives, which includes factors such as climate, habitat, and predators (NMFS 2016). Often times certain life stages are restricted to specific habitat types, and as demonstrated here, early life stages can be highly affected by the physical and biological qualities of pelagic habitats. The inclusion of ecosystem processes and variability of larval fish responses to variable environmental conditions, therefore, may be helpful in developing future EBFM assessments.

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